Post-release behaviour of reintroduced Orangutans *(Pongo pygmaeus wurmbii)* in Bukit Baka Bukit Raya National Park and Bukit Batikap Conservation Forest, Central Kalimantan, Indonesia.

Submitted by Emma Jayne Lokuciejewski to the University of Exeter

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I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

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ABSTRACT

Rescue, rehabilitation and reintroduction programmes are a vital conservation tool used to protect individuals under immediate threat, and then re-establish viable populations in protected habitats. The critically endangered orangutan (*Pongo spp*.) has experienced significant population decline, primarily due to deforestation and hunting, therefore a considerable number of individuals are rescued from fragmented forests or the illegal pet trade. Whilst the protection of the remaining wild populations remains paramount, the substantial number of individuals currently residing in rescue centres means reintroduction is a crucial strategy for reducing the threat of extinction.

Previously, many reintroductions have been ineffective, primarily attributed to inadequate project management, the introduction of unregulated tourism, or due to the individuals' failure to acquire vital survival skills. Furthermore, the lack of post-release monitoring often inhibits analyses of the post-release progress, survival rates, and the long-term effects of human-facilitated rehabilitation. Therefore, the reintroduction of Bornean orangutans (*Pongo pygmaeus wurmbii*) into two protected forests, Bukit Baka Bukit Raya National Park and Bukit Batikap Conservation Forest, Central Kalimantan, provided vital opportunities for understanding how early life experiences and rehabilitation shapes post-release behaviour, ultimately aiding the improvement of reintroduction protocols.

Mixed model analyses of data from consistent post-release monitoring revealed that across the first three months post-release, orangutans displayed behavioural irregularities when compared to their fully-wild counterparts. Temporarily, significantly elevated levels of resting and travelling counteracted reduced levels of feeding, attributed to recovery from transportation and stress from reintroduction into a novel habitat. After approximately three months post-release, behaviour stabilised and closely resembled that of wild orangutans, revealing the robust behavioural flexibility of the species.

Evidence is also provided for distinct dispersal strategies following reintroduction, most notably flanged males were more likely to disperse out of the study site, whilst females often displayed site fidelity and established their home range surrounding their release location. Reintroduced individuals often displayed larger home ranges, when

compared to wild individuals, likely in response to substantial overlaps between individuals around release locations, and subsequent resource competition.

Overall, reintroductions were deemed successful, however, differences in dietary composition were discovered, most notably, lower fruit consumption, and a subsequent increased reliance on fall-back foods. Dietary differences are likely attributed to insufficient foraging skills, therefore improvements to rehabilitation protocols are provided, vital for increasing post-release success. Ultimately, the success of this reintroduction programme, and the establishment of new populations reinforces the value of reintroduction as an effective tool for conservation.

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1.1. INTRODUCTION

Conservation biology seeks to protect and manage biodiversity through the maintenance of genetic variation, species and ecosystems, which have been perturbed directly or indirectly through human activities[1]. Particularly, fragmentation from the destruction of habitats can disturb natural dispersal and population regulation, therefore conservation benefits from developing an understanding of a species' adaptability to human modified environments or degraded landscapes[2]. Anthropogenic effects are driving rapid change amongst flora and fauna, therefore reducing the impact of human activity is paramount for ensuring the preservation of populations under threat. Species already detrimentally impacted face severe population decline, therefore reintroduction is vital for re-establishing new, self-sustaining populations. However, the process of reintroduction can be expensive and time consuming, as many rescued individuals require substantial pre-release training of essential survival skills due to prolonged time in captive environments. The protection and management of release sites also poses further long-term costs, and requires cooperation from authorities and local communities. Nevertheless, reintroduction is crucial to improve the welfare of rescued individuals and to contribute to population restoration in order to reduce the threat of extinction.

To date, many reintroduction efforts have been unsuccessful primarily attributed to the failure to mitigate post-release threats, lack of post-release monitoring, or the animal's failure to exhibit vital survival skills[3]. However, unsuccessful reintroductions provide a foundation, to which improvements can be made. Post-release monitoring is therefore crucial to understand behavioural changes following reintroduction and to identify potential issues, necessary for improving reintroduction protocols and success rates.

1.1.1. Literature review: Factors affecting the success of reintroduction programmes

There are several ecological reasons as to why the intentional, human-mediated movement of animals is a necessary tool for conservation. Firstly conservation

translocation; the movement of an organism from one location to another, is required when wild organisms require movement from a habitat under threat, to a safe, protected area[4]. For example, Black Howler Monkeys (*Alouatta pigra*), faced severe population decline due to a hurricane, yellow fever epidemic and uncontrolled hunting, therefore required translocation to a protected area free from those threats[5]. Secondly, conservation introduction (assisted colonisation) is used to release an organism outside its indigenous range in an attempt to avoid extinction, as demonstrated by the introduction of Tuatara (*Sphenodon punctatus*), into cooler environments in New Zealand, to alleviate the detrimental effects of climate change on temperature-dependent sex determination[6]. Contrastingly, reintroduction is a technique used to release organisms within its indigenous range where the species has been extirpated, or to supplement an existing population[7], such as the reintroduction of Golden Lion Tamarins (*Leontopithecus rosalia*), from severely degraded forests into a protected reserve[8]. Then, supplementing a population is beneficial to increase breeding potential by introducing more genetic diversity and fertile organisms into a small founding population, as demonstrated by the annual reintroduction of Guam Rails (*Rallus owstoni*) into the Northern Mariana island of Rota[9]. However, depending on the target species, reintroduction to supplement existing wild populations may not be practical due to the risk of introducing new diseases or reduced immunity[10]. Overall, the reintroduction of a species into its indigenous range, is beneficial to re-establish self-sustaining, viable populations, and subsequently restore biodiversity. Reintroduction programmes are also beneficial for improved enforcement and awareness of animal protection laws, creating of legal holding facilities for confiscated individuals, and for ensuring the continued policing and protection of habitats[11]. In addition, reintroduction promotes public awareness on the conservation status of the target species, providing education and funding at local and international levels, contributing to their protection[12].

This literature review will focus on reintroductions of species that have experienced significant population decline, exemplifying factors contributing to success or failure whilst highlight the importance of post-release monitoring.

Reintroduction guidelines

Criteria have been formulated by the International Union for Conservation of Nature (IUCN) and conservation biologists to aid the decision making of whether a reintroduction should be implemented, and to improve success rates. Such criteria include determining the necessity of reintroduction, evaluating associated risks, calculating the technical and logistical suitability, and having support from local governments and communities. However, studies have revealed that most projects addressed less than half of these criteria, as they are often inadequately designed[13]. The Association of Zoos and Aquariums (AZA) have also created guidelines offering an extensive list of specific considerations prior to reintroduction such as; sufficient funding, cost-benefit analyses, genotypically appropriate individuals, ecologically suitable release sites, habitat protection, thorough understanding of the species' natural history and behaviour, veterinarian examinations and quarantine to ensure healthy non-diseased individuals are released. Most notably, training of essential life-skills, such as foraging and predator avoidance, and elimination of previous threats are critical criterion to ensure individuals are capable of immediate survival once reintroduced. Then, post-reintroduction criteria include; isolation from wild conspecifics in order to reduce disease transmission, no disruption to ecological balances such as trophic interactions and availability of resources, creation of self-sustaining populations, long-term post release monitoring, and effective management throughout the project[14]. Overall, a multi-disciplinary approach, including social, political and economic factors must be implemented into the guidelines and project design in order to represent the interests of all those involved[7], minimise human-wildlife conflicts[15] and to determine cost effectivity [16,17].

Success and failures

Reintroduction success is highly dependent on the definitions of success used, which vary widely between projects as they depend on the life history of the target species and the project goals. For example, previous studies have defined success as; a three-year breeding population with recruitment rate exceeding death rate[18], an unsupported population of over 500 reintroduced individuals[14], or breeding by release groups and their offspring[19], hence many studies consider the establishment of self-sustaining

populations to be synonymous to success[20,21]. Although, whilst a project may be described as successful at the point of review, changes over time due to the recurrence of original or new threats, may eventually result in failure[19]. Seddon (1999)[19] stated that successful reintroductions should comprise of a sequence of objectives, which span across the life history of the target species. For instance, survival of the reintroduced individuals, breeding by both the reintroduced individuals and their offspring, and subsequent persistence of the re-established population. Similarly noted by Sarrazin (2007)[22], evaluation of success should be divided into releases, growth and regulation analyses, whereby releases and growth phases encompass the short term goals, but regulation is the key indicator to achieving success. Ultimately, successes and failures within reintroduction projects are subjective, as species life history and project goals render many projects temporally restricted and unsuitable for extrapolation across taxa[19], thus it is impractical to standardise a single definition of success[23]. Further, deeming a project as successful, infers that the end point has been reached, implying that further reintroductions and assessments are unnecessary. Nevertheless, despite variations in definitions of success, some projects result in a complete failure due to death of reintroduced individuals, whereas others accomplish population restoration, offering important opportunities for analysing the factors responsible for reintroduction outcomes.

The factors influencing the effectivity of reintroduction must be assessed from the evidence gathered during post-release monitoring. Post-release monitoring allows the behavioural changes, diet and sociality of each individual to be analysed, whilst any potential issues such as illness, or failure to forage can be identified and resolved through medical intervention. Reintroduction protocols can then be adapted or updated to account for newly identified threats, such as human-wildlife conflict, predation or habitat loss. Survival and birth rates can also be quantified from post-release monitoring, allowing assessments of population viability, providing necessary evidence for long-term sustainability. Ultimately reintroduction guidelines provide the key criteria necessary for reintroduction success, whereby pre-release skill acquisition and post-release monitoring are the key criterion to ensure ecological competence in a novel environment. Reintroduction strategies can then be updated in light of the evidence gathered through monitoring, to contribute to the overall increasing effectivity of reintroductions.

To firstly exemplify the significance of adherence to reintroduction guidelines, the reintroduction of Majorcan midwife toads (*Alytes muletensis*)[24], led to the accidental introduction of the *Batrachochytrium dendrobatidis* fungus, which causes Chytridiomycosis, a disease responsible for dramatic declines of amphibian populations worldwide. The captive breeding programme failed to detect the presence of *B. dendrobatidis*, and subsequently reintroduced infected individuals in to the novel Majorcan habitat, creating a mass mortality of the population[25]. This reintroduction attempt failed due to inadequacy of pre-release protocols, highlighting the necessity of following guidelines for disease screening and quarantine periods prior to reintroduction. Likewise, the reintroduction of the Brown Treecreeper (*Climacteris picumnus*), also failed due to the inability to meet predetermined criteria[26]. Low survival rates of reintroduced birds compared to wild conspecifics (15% and 79% respectively) was attributed to increased vulnerability to predation due to sub-standard habitat structure and quality. The release site contained significantly less refuge areas to escape predators, and more obstructive shrubs, when compared to wild sites, emphasising the need for release site viability analyses prior to reintroduction.

To exemplify the importance of monitoring pre-release survival skills

and post-release behaviour, the effective reintroduction of the Yellow-Shouldered Amazon Parrot into Venezuela[27,28] ensured captive birds learned foraging, predator avoidance techniques and alarm vocalisations. This reintroduction attempt addressed the failures of previous similar reintroduction attempts, and resulted in an 83% survival rate, and at least one successful reproduction. Ecological studies on the natural history of the target species were also undertaken, to ensure reintroduction strategies were accurately tailored to the species, whilst veterinary examinations eliminated the chance of disease transmission once released amongst wild conspecifics. Overall, this effective project highlighted the importance of adequate survival skill acquisition prior to reintroduction. Conversely, reintroduced Golden Lion Tamarins (*Leontopithecus rosalia*) in the Poco das Antas Biological Reserve, in Rio de Janeiro possessed inadequate foraging and locomotor skills, when compared to wild-born conspecifics, which led to an increased frequency of falling from climbing substrates[29]. Thus, a combination of intervention in the form of supplementary food, and improvements to survival skill training during rehabilitation are necessary for long-term success. Overall, knowledge of behavioural changes and skill inadequacies post-

release is necessary to improve rehabilitation protocols, in order to ensure each individual is capable of independent survival in a novel environment.

To exemplify the importance of post-release monitoring, data from 51 long-lived, slow-reproducing Western Lowland Gorillas (*Gorilla gorilla gorilla*), reintroduced within the protected Batéké Plateau, in the Republics of Congo and Gabon, determined a 97.4% survival rate, with 11 births, and 81% first year infant survival rate[30]. Comparison with wild populations revealed these demographic parameters were not statistically different, and therefore can be considered an initial success. The project adhered to IUCN guidelines[31] when selecting reintroduction sites with natural barriers between the gorillas and human activity. However, insufficient barriers were later detected but resolved by recapturing gorillas under threat and translocating them to an area with extensive savannahs and rivers between villages, eliminating human-wildlife conflict. Ultimately, the rapid identification of threats via post-release monitoring allowed improvements to be made to reintroduction protocols, paramount for the survival of the population. Conversely, reintroduction of Bighorn sheep (*Ovis canadensis*)[32] created initial high survival rates, however low recruitment rates and subsequent population decline meant a viable self-sustaining population was not established. Population decline was mainly attributed to failure to mitigate the new threat of urbanization as well as the failure to minimise the pre-existing predation threat, and the sheep's subsequent failure to react to the presence of Mountain Lions, or ability to seek escape terrain. Outcomes from this reintroduction attempt also emphasise the importance of identifying new threats via post-release monitoring and updating reintroduction protocols in light of new evidence. Similarly, despite the initial success of Arabian Oryx (*Oryx leucoryx*) reintroduction into Oman, from 10 founders in 1982, to over 400 in 1996, the intensification of poaching caused dramatic population decline, and a subsequent inbreeding depression, leading to a non-viable wild population[33]. By 2007, wild populations continued to decline, and 90% of the reintroduction site was no longer protected, due to the encouragement of oil exploration[34]. Overall, the long-term management of the project failed to protect the population from new threats, highlighting the detrimental effects of insufficient post-release monitoring and evaluation. For species under threat from human-induced factors such as habitat destruction through urbanisation or deforestation, it is vital that

procedures are in place to minimise the damage to habitats and the species depending on them, especially if the threat cannot be eliminated completely[35].

Overall many reintroductions have been ineffective due to an individuals' behavioural inadequacies, or failure to successfully adapt to the release environment, therefore pre-release training and post-release monitoring are key factors influencing reintroduction success. Further, ethical and philosophical complexities arise when determining which populations take precedence, the cost-effectivity of reintroduction compared to wild population protection, and whether reintroductions are merely aiding short-term population restoration, rather than eliminating the initial problem. In general, reintroduction efforts tend to focus on charismatic megafauna, which harbour more public interest and financial support. Nevertheless, utilising the conservation efforts of a flagship species is vital for subsequent ecosystem conservation. Reintroduction should encompass a multi-faceted approach to conservation, via threat mitigation, public education, and habitat protection prior to reintroduction. Then, reintroduction should aim for the establishment of self-sustaining populations, aided by post-release monitoring and regularly updated management strategies to ensure the continued preservation of the population and its environment. Ultimately, recent improvements to reintroduction protocols via the adherence to strict guidelines has led to increased effectivity and subsequent optimism regarding the value of animal reintroductions in conservation.

1.1.2. Study system

1.1.2.1. Orangutan Natural History

The presence of Orangutans (*Pongo spp*.) dates back to the Pleistocene epoch, whereby fossil records depict a widespread distribution across mainland Asia, as far north as China, and throughout South-East Asia[36]. Environmental conditions such as the submergence of the Bangka-Belitung-Karimata land-bridge, separating the islands of Borneo and Sumatra, as well as human encroachment and destruction of their rainforest habitat has severely reduced their distribution[37], and resulted in the IUCN classification of 'Critically Endangered' in 2016[38]. Orangutans are now constrained to the fragmented forests of Borneo and Sumatra, with many separated forests supporting less than 250 individuals, the proposed minimum viable population size[39].

The separation of populations has led to the distinction of three species, *Pongo abelii* and *Pongo tapanuliensis*[40] on Sumatra, and *Pongo pygmaeus* on Borneo[41], of which three sub-species are recognised, *P. p. pygmaeus* within Western Borneo, *P. p. morio* within Eastern Borneo and *P. p. wurmbii* within Southern Borneo[42]. All three species are experiencing population decline, hence the conservation of the species' and their habitat is paramount for alleviating extinction risks[43].

Orangutans are primarily frugivorous, during periods of high fruit availability, but also rely on 'fall-back' foods, such as other plant matter and insects, as a response to fruit scarcity[44,45]. Fall-back foods are defined as those of often relatively poor nutritional value, consumed when preferred foods are scarce, though the most consumed fall-back foods differ across species and forest types[45]. For example, Bornean orangutans tend to rely heavily on the inner cambium of certain plants, whereas Sumatran orangutans rely heavily on higher-quality figs[46]. Orangutans therefore primarily reside within lowland dipterocarp forests, peat-swamp and freshwater-swamp forests, and alluvial forests within river basins, areas with a sufficient abundance of food. Subsequently, the large body size of orangutans and frugivorous diet favours a semi-solitary lifestyle in order to reduce food competition[47], whereby individuals roam over large areas, often overlapping with neighbouring individuals, but only associate occasionally within fruiting trees[48], or for mating opportunities[49,50].

Geographic variation in behaviour exists across the *Pongo* taxa, whereby from west to east home range size and daily distance travelled decreases, whilst the reliance on 'fall-back' foods increases, due to individuals covering smaller areas [51]. Sumatran orangutans also display a higher level of sociality than Bornean orangutans, though variation exists within the Bornean subspecies. Variation in behaviour is often attributable to habitat differences, whereby more productive forests with a temporally consistent supply of food, particularly in Sumatra, allow a diet of higher fruit consumption, a high degree of range overlap, and in turn, increased sociality[51]. Further, the presence of tigers on Sumatra means Sumatran orangutans are at a higher risk of predation, therefore tend to remain arboreal, in comparison to Bornean orangutans, particularly flanged males, who commonly travel terrestrially[52].

Despite a semi-solitary lifestyle, orangutans utilise social learning in addition to independent learning via trial-and-error, to develop their foraging skills and dietary

repertoire, particularly during the infancy period[53,54]. Orangutans remain in close association with their mothers until weaning at approximately six to nine years old[55], whereby offspring develop gradual independence, though may establish an overlapping home range[56]. Prolonged association between mother and infant provides critical opportunities to learn complex foraging techniques, predator avoidance behaviours and skills necessary for independent survival[57]. In particular, infants gain information on edible food types, particularly those requiring complex skills to obtain, through observations and food transfer from their mother[58], then continue to exhibit similar diets post-weaning[53]. Infancy is therefore a critical period for survival skill acquisition via social learning.

1.1.2.2. Orangutan conservation and reintroduction

The most prolific problem facing primates, specifically great apes across Africa and South-East Asia, is human-induced habitat destruction, resource depletion, poaching and the illegal pet trade[59]. According to the IUCN Red List of Threatened Species, 33% of the 48 species of non-human primates in Indonesia are classified as Vulnerable, whilst 31% are Endangered, and 19% are Critically Endangered, all with populations in decline[38]. Rescuing animals under threat can pose challenges at local and governmental levels, as illegal activity often occurs. The illicit trafficking of primates has developed into a sophisticated network of dealers, capturing primates from the wild for bushmeat, the illegal pet trade, and for international trade[60]. 22,218 great apes are lost annually due to the illegal trade, however legal repercussions to the offender are often lacking, as only 27 arrests were made across Asia and Africa between 2005 to 2011, of which a quarter were never prosecuted[61]. Specifically for Orangutans, 440 formal confiscations occurred between 1993 and 2016, resulting in only seven prosecutions which held lenient sentences[62].

Habitat destruction for logging and conversion for oil palms (*Elaeis guineensis*), remains a prominent threat to orangutans. Palm-oil is the highest-yielding, and least expensive vegetable oil, hence it is the preferred crop for meeting the high demand of the increasing human population[63]. Driven by the demand for this commodity, the expansion of the palm oil industry by large-scale plantations and small-holder schemes, has already rapidly increased the scale of deforestation, and is projected to

continue to increase further[64]. As one of the main causes of forest loss on Borneo, the need for increased sustainability of palm-oil is pivotal for reducing the destruction of the last remaining orangutan habitats[65]. The Roundtable on Sustainable Palm-Oil (RSPO) was therefore established to produce global standards for sustainable growth and use of palm oil, prohibiting deforestation[66,67]. Hence, orangutans rescued from areas deforested for palm-oil reveals the corruption and illegality of plantations concessions, as many plantation owners are members of the RSPO[68], committed to ensuring that biodiversity is maintained[69].Furthermore, orangutans have been a protected species under Indonesian law since 1931[62], yet hunting due to agricultural conflict, for the illegal pet trade, or for consumption, still persists[70,71]. Consequently, rescues and confiscations are complex, and to be successful, require collaboration from local people, NGOs and Governments[72].

Humans have influenced the ecology and distribution of orangutans for at least 70,000 years, primarily due to deforestation for agriculture, though recent studies have emphasised the robust adaptability of the species, allowing them to survive in degraded and human-modified environments[2,73]. Though orangutans exhibit behavioural flexibility in response to habitat degradation, large scale poaching and the illegal pet trade remains an imminent threat to which they are unable to respond. Organisations created specifically for the purpose of rescue, rehabilitation and reintroduction, are therefore established as an immediate response to wildlife exploitation. However, orangutan reintroduction is inherently expensive, costing around $44,121 per successful individual[74], 12 times more than forest protection, and is only cost effective across short time scales, therefore is not sustainable. On the other hand, forest protection harbours complex conservation and land-use issues, making it difficult to achieve. Whilst protection and preservation of wild populations remains paramount for conservation, the vast number of individuals already in rescue centres or under immediate threat means reintroduction accounts for a substantial number of the remaining population, and is therefore an integral part of conservation. Subsequently, a combined strategy of rescue, rehabilitation, and reintroduction of those under immediate threat, and long-term protection of wild populations is critical for orangutan conservation.

Early conservation efforts released rescued orangutans amongst native populations, in the hope that they would integrate with wild conspecifics and learn wild behaviours,

whilst boosting population numbers, however this resulted in disease transmission, over population and social stress[75,76]. In the 1990s Rijksen developed a new method for orangutan conservation, termed ‘reintroduction’, emphasising that orangutans must be released in areas without a resident, wild population, which was met with improved effectivity[75,76].

Between 1964 and 2009 over 1000 rescued orangutans were released either into existing populations, or into protected forests without native orangutans, representing 2-3% of the overall population[2,11], though this number is likely now an underestimate due to the continuous influx of rescued orangutans, and decreasing wild population. As of 2018, there are 11 active rescue and rehabilitation centres, and 10 active reintroduction sites (TNBBBR, Batikap, Kehje Sewen, Gunung Tarak, Lamandau Reserve, Bukit Tigapuluh, Jantho Nature Reserve, Kabili-Sepilok Reserve, Tabin Wildlife Reserve and sites bordering Tanjung Putting National Park), all exhibiting varying degrees of success[11]. Six former reintroduction sites are no longer in use (Tanjung Putting, Sungai Wain, Meratus, Bukit Lawang/Bohorok, Ketambe and Semenggoh), due to ineffective reintroduction strategies or reaching carrying capacity.

Bukit Lawang in Sumatra, and Sepilok, Camp Leakey (Tanjung Puting) and Semenggoh in Borneo have attracted large influxes of tourists to the rehabilitation centres and release sites since the 1970s, initially to increase public interest in orangutans and to generate funding for their conservation[77,78], however the role of tourism in orangutan conservation has since been debated. The economic value of tourism is outweighed by the increased risk of disease transmission[79], increased human dependence[78] by overreliance on provisions[80], and decreased survival rates[11], overall proving detrimental to reintroduction success.

Reintroductions of Sumatran Orangutans (*Pongo abelii*) into Bukit Lawang, Sumatra, a site with high levels of unregulated tourism presence, has resulted in an abnormally high level of infant mortality (56%), human-transmitted disease, and two unrelated occasions of mother-infant cannibalism[81]. This abnormal behaviour has never been documented in wild orangutan populations and may therefore be attributed to trauma prior to rehabilitation, poor parental skills, failure to reduce human dependence, or behavioural disruptions due to the presence of unregulated tourism[82].

Reintroductions from Sepilok Orangutan Rehabilitation Centre, in Malaysian Borneo, studied between 1967 and 2004 revealed 14 females produced 28 offspring, however a high infant mortality rate of 57% was recorded[83], with an abnormally high sex ratio biased towards females, attributed to poor health of mothers and social stress due to provisioned feeding platforms. In 2010, three more individuals were reintroduced, using a hard-release strategy consisting of no supplementary food, then five were released in 2012 with food provisioned on an ad-hoc basis[84]. In total, one birth was recorded, and all individuals managed to integrate with resident wild orangutans, resulting in a partially successful evaluation by the IUCN[85], although reintroduction amongst wild orangutans is no longer endorsed. However, two individuals from the hard-release strategy were confirmed dead, within first year, highlighting the necessity of acquiring independent foraging skills prior to release.

Camp Leakey in Tanjung Puting National Park, Borneo, released orangutans amongst wild conspecifics since the 1970s, however failed to record the number released individuals and their outcomes[86]. The continuation of unregulated tourism has now proved that Camp Leakey operates as a tourism attraction rather than conservation organisation. Most notably, the use of feeding platforms has meant rehabilitants have become reliant on provisions rather than exhibiting natural foraging behaviour, which in turn has affected ranging behaviour[86]. Furthermore, feeding platforms and boardwalks act as tourist hotspots, whereby the public can view, and often interact with rehabilitants, posing risks for disease transmission and over habituation[87]. Overall inadequate management, and failure to adhere to IUCN guidelines[14] has led to the failure of this reintroduction attempt. Similarly, studies at Semenggoh Orangutan Centre in Malaysian Borneo, have revealed that the presence of orangutans provides an economic benefit to Malaysia, though the funds are generated through the use of captive orangutans as tourist attractions, rather than wild populations[88]. Hence, many sites such as Bukit Lawang, Sepilok, Camp Leakey, and Semenggoh are reluctant to shift their focus from tourism to conservation, due to the inevitable economic loss[87].

Rehabilitation and reintroduction without tourism therefore focusses on animal welfare and conservation. For example, the Wanariset Orangutan Reintroduction Project (Samboja Lestari) in Borneo, reintroduced 88 orangutans into the Sungai Wain forest, and 345 into the Meratus forest, between 1992 and 2002[89], however the lack of post-release monitoring meant less than 20 individuals were re-sighted during subsequent

studies in 2009. Overall, inadequate skill acquisition during rehabilitation and lack of monitoring were responsible for reduced success of this project.

Despite the litany of failures within previous reintroduction attempts, some programmes have proved highly effective. For example, Bukit Tigapuluh, the reintroduction site of the Sumatran Orangutan Conservation Programme has no resident wild orangutan population, and covers 144,000 hectares of lowland dipterocarp forest, offering ideal conditions suitable for over 1000 individuals[11]. Results from eight reintroduced individuals suggest behavioural differences amongst human-bonded immature rehabilitants owing to their affinity to humans, whilst those who actively avoided human contact acquired superior survival skills, comparable to wild orangutans[90], emphasising the importance of gradual weaning from human carers. Further studies revealed reintroduction success owing to high survival rates, the establishment of a new population, and three successful wild births, from the 100 individuals reintroduced[91]. This project exemplifies reintroduction success, thus improving the prospects of future reintroductions.

Through reviewing factors responsible for the outcome of previous reintroduction attempts, predominantly, tourism, acquisition of vital survival skills, and post-release monitoring, some programmes have developed effective and successful reintroduction strategies. Overall the effects of tourism have been proven detrimental to pre-release and post-release progress, due to the risks of disease transmission and behavioural inadequacies. Programmes without a tourism presence have shown increased effectivity, though post-release monitoring is often lacking. Ultimately, improved, well documented reintroduction protocols have resulted in substantial success, reinforcing the value of reintroduction as a tool for conservation.

1.2. RESEARCH METHODS

1.2.1. Borneo Orangutan Survival Foundation's rehabilitation and reintroduction protocols

Most rescued orangutans are wild-born infants under the age of three, orphaned as their mothers were killed during poaching or deforestation. Infants are often taken from their mothers and sold through the illegal pet trade, often enduring inadequate conditions. As a consequence, many suffer physical and/or mental disabilities as a result of the past traumatic experiences. Further, orphaned infants are deprived of the essential mother-infant bonding and early-life, social learning experiences, therefore lack the critical skills needed to independently survive in the wild. Rehabilitation is therefore necessary to provide individuals with the essential survival skills, such as foraging, climbing, nest building and predator avoidance, which their mothers would have otherwise taught them. Previous studies have confirmed captive orangutans show preference to learning from caregivers or group members, therefore rehabilitation provides multiple opportunities for skill acquisition[92–94]. Orangutan rehabilitation must therefore encompass the period from infancy to independence to ensure individuals gain all skills necessary for independent survival.

At the Borneo Orangutan Survival (BOS) Foundation's rescue and rehabilitation centre, Nyaru Menteng, in Central Kalimantan, rehabilitation involves training former captive individuals to successfully behave, survive and reproduce in a wild environment, through the use of human caregivers or similar-aged conspecifics. Rehabilitation may also involve medical treatment for physical and mental disabilities, until healthy enough to survive without human interference. Individuals under two years of age are housed in a 'nursery' facility, allowing them to received 24-hour care, whilst playing with conspecifics and learning basic skills. Individuals between the ages of two to five learn key survival skills through 'forest schools' whereby groups of individuals are taken into a secure area of forest, and trained to recognise, collect and ingest provisioned and wild food items, interact with conspecifics in a natural manner, gain ecological skills, and avoid predators, through observation and teaching by caregivers. Previous studies at Nyaru Menteng revealed, both provisioned food items (n=32) and natural forest food items (n=83), are available during forest school[54], allowing individuals to learn wild food sources as well as ensuring full daily nutritional

intake. The variation in types of food provisioned during rehabilitation varies depending on the availability of local produce as vast quantities are needed to supply large rescue centres. Mostly, provisions consist of bananas, oranges, cucumbers, leaves, corn, sugar cane, tofu and tempeh, cultivated foods which are typically unavailable in the forest. Individuals rescued over the age of 5 have often endured significant time in isolated captivity, and are too mature to join forest school, therefore are placed in provisioned socialisation cages to interact with other orangutans.

Upon completion of forest schools, gradual weaning from human carers is then necessary to ensure independence[95], as they are transferred to socialisation cages, then pre-release islands, a semi-wild environment whereby individuals are free to independently roam and forage on wild food items, as well as take provisioned food at feeding platforms. Reintroduction candidates must exhibit key survival skills such as independent foraging, nest building and predator avoidance skills, to ensure the best chance of survival upon release. On average, individuals at BOSF spend 10 years in rehabilitation, from point of rescue to reintroduction, with 2-3 of these years being on a semi-wild pre-release island, however this time scale varies depending on the progress of the individual. Due to the detrimental effects of food provisioning recorded at previous reintroduction sites, a hard release strategy is implemented by BOS, whereby provisioned food is not available for orangutans once reintroduced into the wild. As food is a main factor affecting primate survival, it is imperative that rehabilitation encourages individuals to exhibit fully independent foraging on a variety of fruit and fall-back food items prior to reintroduction[96].

Prior to reintroduction, individuals are fitted with subcutaneous radio telemetry implants, to aid locating individuals for post-release monitoring, and given a veterinary examination to confirm healthiness. Reintroductions are designed to loosely mimic the spatial and demographic organisation of a natural population, with a density of 1.5 individuals per square kilometre, and flanged males evenly distributed amongst females. Small groups of 5-6 individuals are released at approximately two to three-month intervals, to ensure all individuals can be monitored across the crucial first weeks post-release. Release groups are distributed 1-2km apart to avoid overcrowding, and veterinary assistance or supplementary feeding is available if medically necessary.

1.2.2. Study sites

Figure 1.1. Map of Borneo and the locations of Bukit Baka Bukit Raya National Park (TNBBBR), the Muller Ecosystem (containing Batikap) and Nyaru Menteng Rescue and Rehabilitation Centre.

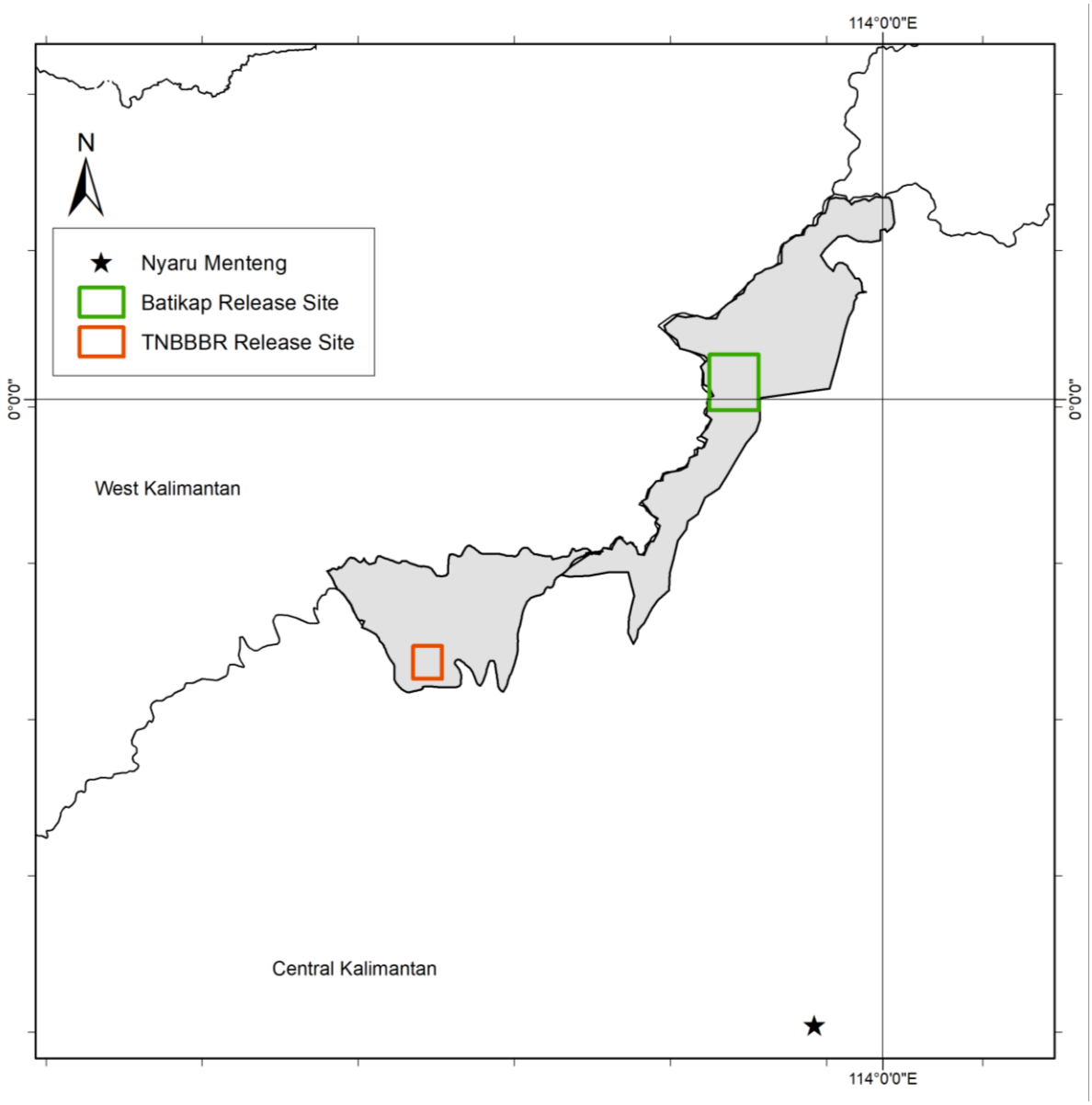

Figure 1.2. The locations of the TNBBBR and Batikap release sites, and Nyaru Menteng Rescue and Rehabilitation Centre.

Bukit Batikap Conservation Forest

The first reintroduction site is located in the Bukit Batikap Conservation Forest, in the Murung Raya District, part of the Muller Ecosystem, Central Kalimantan, Borneo (0º2'N, 113º31'E)[97], hereby referred to as Batikap (Figure 1.1). Batikap lies amongst the Muller-Schwaner mountain range, encompassing 35,267 ha of lowland primary rainforest, with 4,800 ha of homogenous mixed dipterocarp forest between 200-500m above sea level (asl) covering the study site (Figure 1.2). The area surrounding Batikap is protected due to containing a major watershed with areas of forested

plateaus, forming one of the largest tracts of unbroken rainforest in the world. The Muller Ecosystem acts as an ecological corridor, connecting Bukit Batikap Conservation Forest to Bukit Baka Bukit Raya National Park.

Aerial flyover assessments were conducted in April 2011 to determine the extent of human activity, forest types and natural boundaries. Land surveys in June 2011 revealed suitable forest composition, with a high diversity of food types and received support from neighbouring villages, concluding suitability for reintroductions. A monitoring camp, helipad and grid system of transects were constructed to assist orangutan releases and subsequent long-term monitoring (Figure 1.3). Post-release monitoring data has been consistently collected by a team of local field assistants and scientific researchers since the first reintroduction in February 2012.

Figure 1.3. The transect grid system, release points and major rivers within the Batikap release site.

Bukit Baka Bukit Raya National Park

The second study site is located in Bukit Baka Bukit Raya National Park (0°52'S, 112°30'E), which straddles the border of Central and West Kalimantan, hereby referred to as TNBBBR (Figure 1.1). The 236,000 ha national park lies amongst the Muller-Schwaner Mountain range, which contains the two highest mountains in Kalimantan, Bukit Baka and Bukit Raya. The reintroduction site is to the South of the National park, within the lowland forest at the foothills of the mountains <250m in altitude (Figure 1.2). The site is a homogenous mixed dipterocarp forest of hilly terrain, surrounding the Bimban river, with a carrying capacity of approximately 200 orangutans, providing opportunities for dispersal and population growth throughout the national park. This area was chosen due to accessibility to Nyaru Menteng, ecologically suitable habitat, and being logistically possible for both release and post-release monitoring.

Prior to reintroduction into TNBBBR, aerial flyover assessments revealed habitat suitability, due to there being no signs of human activity in the majority of the park, high mountainous borders, no adjacent settlements and diverse forest cover[98]. Ground surveys revealed some orangutan nests, suggesting very small orangutan density of less than 0.2%, most probably an adult male dispersing through from the small, non-viable, wild population surrounding Bukit Baka[99], but no viable wild orangutan population is present within the reintroduction site. Phylogeny surveys revealed 6% dipterocarps, 276 non-dipterocarps, 48 lianas and three figs per hectare. The area has been disturbed by illegal logging since the end of the 20th Century, however 139 tree species were identified, 126 of which are potential fruit sources, concluding suitable habitat for orangutan reintroductions. There is also positive community support, expressed in socialisation visits to the local villages. Reintroductions into TNBBBR were then initiated in August 2016, after a basic research camp, and a grid system of transects were constructed (Figure 1.4), followed by consistent post-release monitoring conducted by a team of local field assistants.

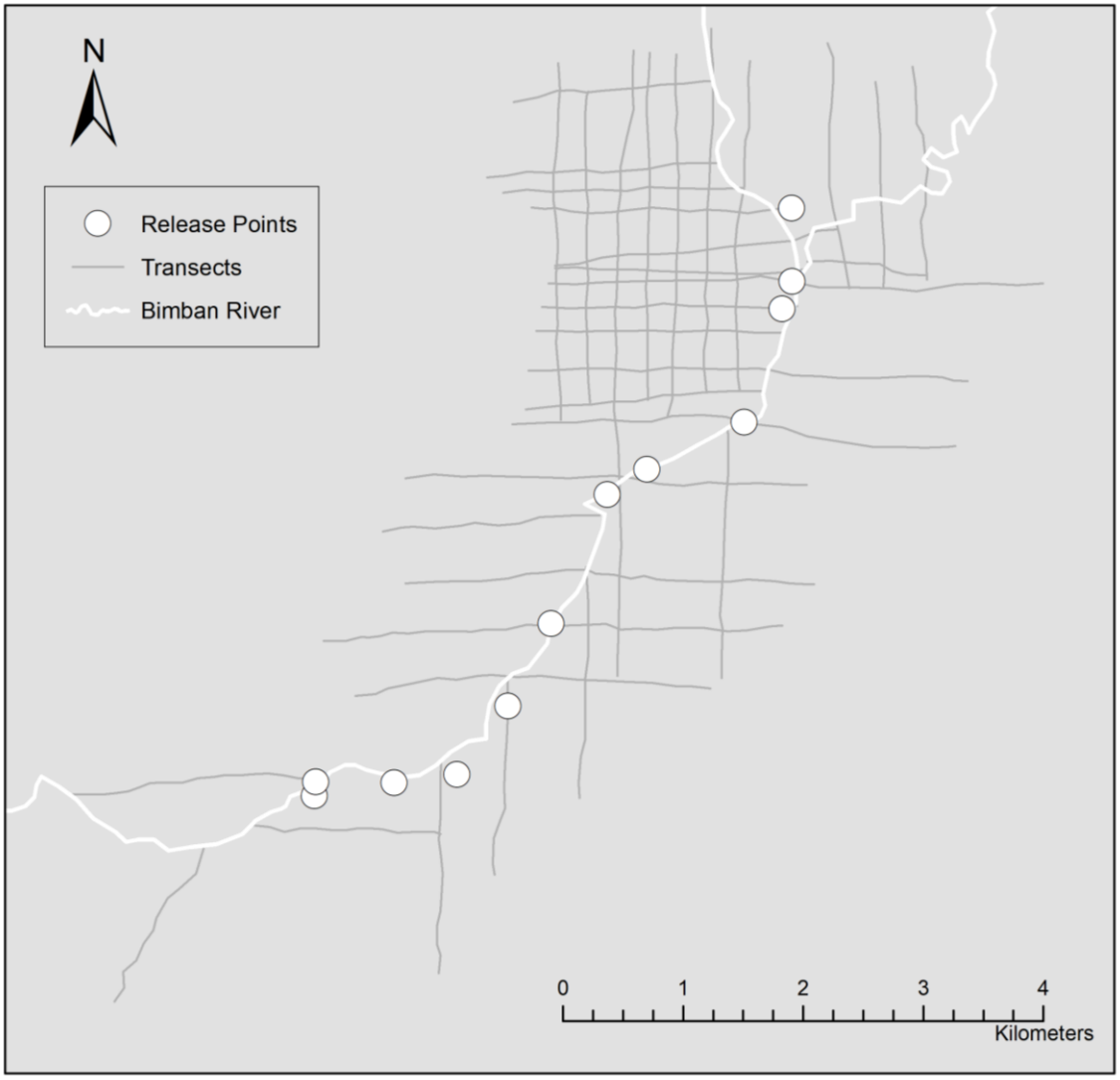

Figure 1.4. The transect grid system, release points and major rivers within the TNBBBR release site.

I aided data collection at TNBBBR between February and August 2017 alongside field assistants, and used all data collected from August 2016 to January 2018 in TNBBBR and from February 2012 to April 2018 in Batikap for analyses to increase sample size. No data were available from wild orangutans in a homogenous mixed dipterocarp forest in Central Kalimantan to provide an equivalent environment comparison, therefore comparisons to wild populations in a homogenous forest, and in a mixed dipterocarp forest were conducted separately. Limitations exist through comparing populations in different forest types, such as differing food availability, however multiple comparisons in different environments allow consistent similarities and trends to become evident. Therefore, I used raw data collected by Borneo Nature Foundation

at Sabangau National Park, Central Kalimantan (2°19′S, 113°54′E), for home range comparisons to wild orangutan populations in a homogenous forest, and data from The Gunung Palung Orangutan Program in Gunung Palung National Park, West Kalimantan (1°13'S, 110°7'E) for comparisons to wild populations in dipterocarp forests.

Study subjects

The profiles of each individual reintroduced into Batikap and TNBBBR are available in Appendix A and B respectively, including release group, release date, Age-sex class, origin, age at rescue and age at release.

Chapter 2: Longitudinal analyses of post-release behaviour of reintroduced orangutans (*Pongo pygmaeus wurmbii*)

2.1. ABSTRACT

Rescue, rehabilitation and reintroduction is a key conservation tool, used to protect individuals under immediate threat from factors such as deforestation or poaching, then re-establish viable populations in the wild[100,101]. However, the effectiveness of reintroduction is often questioned, due to many previous failed attempts. Longitudinal changes in post-release behaviour of reintroduced individuals have rarely been examined, but are vital for understanding the influence of early life experiences and rehabilitation on post-release success. Post-release monitoring of reintroduced orangutans in Bukit Baka Bukit Raya National Park, and Batikap Conservation Forest, Central Kalimantan, Indonesia, revealed temporary behavioural abnormalities, such as a significantly reduced foraging effort, elevated levels of resting and travelling, as well as increased sociality, during the first three months post-release. Then, after approximately three months post-release, behaviour stabilised, resembling that of their fully-wild counterparts, resulting in the identification of distinct 'adaptation' and 'stabilisation' periods. However, dietary analyses revealed lower fruit consumption when compared to wild populations, suggesting improvements to rehabilitation protocols are necessary to improve foraging skills and post-release diet. Overall reintroduction success reinforces the value of reintroduction as an effective tool for reducing the threat of extinction.

2.2. INTRODUCTION

Anthropogenic effects are a key factor influencing the population decline of many species, therefore, habitat protection and threat reduction is vital to ensure the long-term persistence of the species. Then, alongside the reduction of threats such as deforestation or hunting, rescue, rehabilitation and reintroduction can be an essential tool for ensuring the survival of endangered species. Furthermore, reintroduction can then aid the re-establishment of self-sustaining, protected populations, contributing to the conservation of the species. To date, reintroduction has been used for a variety of taxa but their success has been highly variable, therefore research focussing on

factors influencing reintroduction outcomes are essential for improving success rates[102].

Individuals rescued at an early age, often rely on rehabilitation in order to learn the crucial survival skills that they would have otherwise learned from their parents or conspecifics. For the critically endangered orangutan (*Pongo spp*.), large-scale habitat destruction by deforestation and the illegal pet trade has created an influx of orphaned individuals in need of rescue[103]. Orangutans are dependent on their mother for food, protection and survival skill acquisition, for between six and nine years, until gradual independence is exercised[57]. Rehabilitation must therefore encompass the infancy period, providing individuals with the opportunity to learn all essential survival skills, prior to reintroduction into wild habitats. Then, the aim of reintroduction is to create self-sustaining, healthy populations in protected areas, free from human intervention. Whilst protecting the remaining wild orangutan populations remains paramount, the number of rescued individuals represents 2-3% of the total population[2], meaning rehabilitation and reintroduction is a key conservation tool for reducing the threat of extinction.

Orangutan reintroduction has been an active conservation tool since the 1960s, though has often proved ineffective[11]. For instance, previous reintroduction attempts have often involved tourism in order to raise funds, however, this has detrimentally affected pre-release and post-release progress, due to the increased risk of disease transmission and behavioural abnormalities influenced by the presence of unregulated tourists[86]. Moreover, reintroduced individuals have often lacked critical survival skills, such as the ability to forage efficiently, limiting their ability to survive independently once reintroduced. Changes to rehabilitation protocols may reduce these problems, by eliminating the risks associated with tourism and providing the animals with opportunities to build and improve critical survival skills. The adherence to the IUCN guidelines has improved effectivity, exemplified by the Sumatran Orangutan Conservation Programme achieving the highest survival rate of any primate reintroduction programme[3]. However, the extent to which orangutans are able to adapt effectively to life in the wild is unclear due to lack of post-release monitoring. Therefore, longitudinal monitoring of the behaviour of individuals following release is now critical to evaluate and improve the success of reintroduction programmes.

Reintroduction is expected to effect initial post-release behaviour as reintroduction into an unfamiliar environment without food provisions is likely to invoke a stress response[104], however, how individuals adapt to the environment across time is of particular interest. I hypothesised that newly reintroduced orangutans will take a period of time to adjust to the novel environment before maintaining a stable activity budget. To investigate this, I used longitudinal monitoring of behaviour and diet to analyse initial responses to reintroduction, and then subsequent behavioural stability. I also hypothesised that reintroduced orangutans would exhibit behavioural differences, when compared to wild orangutans, in particular, increased sociality and inferior foraging skills due to prolonged time spent in rehabilitation. I used data from comparable wild populations as a basis for expected post-release behaviour, to analyse the influence of rehabilitation. I used activity budgets, displaying the amount of time an individual spends exhibiting different activities, as a means of evaluating daily behaviour of each individual. In particular, time spent feeding provides information on both the habitat quality and foraging behaviour, whilst time spent travelling can indicate the level of exploratory behaviour, necessary for understanding how individuals interact with their environment.

The origin of rescued individuals, such as *rehabilitant*, *semi-wild* or *born on island* relates to the retainment of wild behaviour and key survival skills. For example, *rehabilitant* individuals, those rescued during infancy, often orphaned, have limited knowledge and skills for independent survival therefore need to learn key survival skills through rehabilitation. On the other hand, *semi-wild* individuals, are defined as those who at the time of rescue, had previously encountered humans, but retained sufficient survival skills and behaviours to survive independently in the wild. Finally, infants born on pre-release islands will initially learn survival skills from their rehabilitant mothers, in a semi-wild environment, then develop independence in the wild. I therefore examined the effects of origin on feeding rates of reintroduced individuals. Furthermore, as age at rescue relates to the attendance of forest school and overall amount of time spent in rehabilitation, I also examined their effects on feeding levels. Finally, I examined the effects of feeding levels on survival rates to further investigate the critical factors responsible for reintroduction failure.

A large body size and frugivorous diet means orangutans primarily roam independently to reduce resource competition and subsequent food source

exhaustion[47]. However, social aggregations do occasionally occur within travel bands[105] and mating consorts[106,48], and temporary passive aggregations occur surrounding fruiting trees during periods of high fruit abundance[107]. Wild females tend to associate mostly with neighbouring individuals, often offspring or other relatives, termed a 'cluster'[108], rather than unfamiliar individuals, whereas males tend to pursue sexually active, non-related females[109]. Hence, differences in early life social conditions, and artificially created distributions upon reintroduction are expected to increase post-release social interactions. Understanding who individuals are associating with and why, is key to understanding the influence of forest schools. Further, as there is no known relatedness between rehabilitants, there should be no kin-based spatial structure following release. I therefore predict that individuals will associate with known individuals whom they progressed through rehabilitation with, rather than unfamiliar individuals, similar to the social tolerance recorded between related wild individuals[108,110].

Factors effecting reintroduction success can be taxon specific, such as predation risks[111], presence of human-wildlife conflicts[112], or susceptibility to parasitism[113]. However, inadequate pre-release training, lack of threat mitigation and lack of post-release monitoring are key factors responsible for reintroduction failure, shown across many reintroduction attempts[100]. Ensuring individuals are capable of independent survival, then allowing individuals to adapt to local habitats prior to reintroduction, are critical requirements prior to reintroduction. Then, reintroducing individuals into areas where wild populations are absent, will further benefit long-term success rates[114]. For primates in particular, food is a key factor affecting survival[11], therefore understanding the diet of wild orangutans is important for investigating the ecological requirements of a population, as well as habitat quality and suitability for reintroductions. Understanding dietary breadth and composition of reintroduced orangutans is then necessary to analyse the influence of foraging skill acquisition and provisioned food during rehabilitation, on post-release diet.

Finally, comparing behaviour at reintroduction sites reveals whether trends seen are consistent, despite differences in reintroduction locations. Then, comparing reintroduced populations to wild populations reveals the similarities and differences between observed and expected behaviour, key to evaluating reintroduction success.

2.3. METHODS

2.3.1. Study sites and subjects

Data from the Borneo Orangutan Survival (BOS) Foundation's Central Kalimantan reintroduction sites in Bukit Baka Bukit Raya National Park (TNBBBR) (0°52'S, 112°30'E) and Bukit Batikap Conservation Forest (Batikap) (0°2'N, 113°31'E), were analysed, then compared to published data from other reintroduction sites and from wild populations. Both reintroduction sites are homogenous lowland mixed dipterocarp forests. The study subjects have all undertaken stages of rehabilitation, though their age at rescue influences the time spent in rehabilitation (See Appendix A and B for subject profiles). All reintroduced orangutans are fitted with a small, Very High Frequency (VHF) radio transmitter implanted subcutaneously on the dorsal neck region[115], to assist locating individuals for post-release monitoring. The device poses no adverse effects to the behaviour or health of the individual[84].

2.3.2. Data collection

Behavioural data are collected using the focal animal technique[116] by instantaneous sampling at five minute intervals[117] conforming to the BOS Standardised Operating Procedures, which are based on the Sabangau orangutan behaviour Standard Operating Procedures 2016[118]. Data is recorded using an ethogram encompassing all behaviours orangutans are known to exhibit (See Appendix C). Primary activities, in order of priority include; feeding, nest building, social behaviours, mating, aggressive-dominance, social playing, social grooming, other social activities, aggression to another animal, aggression to observer, infant behaviours, travelling, self-grooming, and resting. Secondary activities consist of further details of the primary activity, such as the species of food item and parts of the food eaten, type and height of nest built, type and purpose of social behaviours, mode of travel, or rest substrate. If multiple behaviours occur simultaneously, the behaviour that is higher in the order of priority takes precedence. Height in the tree, party size, members of party and numbers of kiss squeaks (alarm call) is also recorded at each interval, along with notes of any

other interesting behaviours. The same observer collected data for the full follow to reduce observer bias.

Follows were either initiated when the individual was located via radio telemetry and visual searching, or at the start of the active period. The start of the active period is defined by standardised field protocols as "*the time of day when animal first sits up at the edge of the nest (or performs a behaviour other than reclining)*"[118]. Follows ended when an individual reclined in a night nest and ceased all further activities, or was lost due to adverse weather conditions or significant travel distance, hence a follow covering the entire active period is termed 'nest-to-nest'.

2.3.3. Data analysis

Analyses were conducted within R version 3.4.3[119]. Linear mixed models (LMM) and Generalised linear mixed models (GLMM) were run using the *lmer* and *glmer* functions in the '*lme4*' package[120]. Normality and homogeneity of variance were checked by visual inspection of residual plots and Bartlett's tests. To account for repeated measures of individuals across time periods, individuals were fitted as a random factor in all models. Results were calculated by likelihood ratio tests of the full models against a simplified model without the fixed effect in question. I then called upon the summary() function in the "lmerTest" package[121], to obtain p-values and degrees of freedom, which were not otherwise available from the *lme4* package. The significance threshold was set at $\alpha=0.05$. Full tables of statistical results from mixed model analyses are given in Appendix E, F, G and H. Behavioural data from TNBBBR consisted of 71 individuals, from eight release groups, up to 18 months post-release. Data was collected between August 2016 and January 2018, totalling 5328 hours of observations, from 723 individual follows, with a mean follow length of 7.28 hours. Two follows from TNBBBR were eliminated due to being of a sick individual receiving veterinary intervention and supplementary food. Data from Batikap consisted of 115 individuals, from 12 release groups, up to 69 months post-release. Data was collected between February 2012 and April 2018, creating a total of 11310 hours of data, from 1657 individual follows, with a mean follow length of 6.77 hours. All follows were greater than three hours in length.

2.3.3.1. Activity budgets

Orangutans spend the majority of their daily activity budget either feeding, resting or travelling, with minimal time spent nest making, and only rare instances of exhibiting other activities, such as social interactions[44], therefore the following analysis is limited to the three main activities, with all remaining activities grouped together under the category 'other'. The time spent feeding, resting, travelling and exhibiting other activities was calculated as a percentage of daily activity budget by totalling the amount of time the individual was recorded exhibiting the behaviour, over the total follow time, to account of variation in follow lengths. To account for some individuals not being followed for each consecutive month, a 3-month period (trimester) was implemented as a suitable time period for more robust comparisons between individuals over longer time frames, illustrating the general trends. Then, monthly periods were used to gain a more detailed understanding of initial responses within the first trimester.

I classified individuals into Age-sex categories, consistent with widely used classifications[44,110,122–124], to differentiate between morphological differences between individuals. Females are categorised as either 'sexually active' (SAF) or 'non-sexually active' (NSF), and males are categorised as 'flanged' (FM) or 'unflanged' (UFM). Sexually active females are defined as sexually mature, parous adults, either accompanied by an infant or without offspring as a result of juvenile independence, or early death of the infant. Non-sexually active females are defined as sexually maturing or mature, nulliparous females, travelling independently. Flanged males are defined as morphologically distinct, mature males, displaying fully developed cheek-pads (flanges), laryngeal throat sacs and larger body size. Unflanged males are defined as sexually maturing or mature males undergoing developmental arrest, therefore do not display flanged traits, though early signs of cheek-pad development may be visible.

To firstly identify the general trend of behavioural changes across time, I compared the mean percentage of time spent feeding, resting and travelling across trimesters, for TNBBBR and Batikap. Data from full day 'nest-to-nest' follows as well as partial day follows were included in analyses, however follows less than three hours long were eliminated due to not being representative of daily activity budgets[118]. Separate analyses using only follows >3 hours, >6hrs and only full day 'nest-to-nest' follows

were compared, but gave the same trends, therefore the larger data set was preferred[123]. As individuals were reintroduced in groups, in separate locations, at approximately 2-3 month intervals throughout the year, release group was also included as a random factor. 3-month post release 'trimester' and Age-sex classification were incorporated as fixed effects. Using the ANOVA function, likelihood ratio tests were calculated for the significance of 'Trimester' and 'Age-sex' classification on activity budgets, by comparing full models to simplified models (without explanatory variable). Tukey post-hoc tests with Bonferroni corrections were then used to determine significant pairwise differences between variables. Then, to determine whether release site influenced activity budgets, Welch's two-sample t-tests were used compare activity budgets between TNBBBR and Batikap.

To focus on the effects of rehabilitation on feeding levels, individuals were categorised into sub groups depending whether they are rehabilitant, semi-wild, or born on pre-release islands. To further investigate the effects of forest-schools on feeding levels, the individuals that had the necessary data available were categorised into sub-groups depending on their age at rescue, which coincides with attendance to the various stages of rehabilitation. Using only time spent feeding, linear mixed models[120] were applied using individuals in TNBBBR and Batikap combined, with sub-groups used as fixed effects, and month post-release and individual incorporated as random effects. Finally, to confirm the effects of feeding levels on survival rates, the feeding levels of individuals who had successfully survived independently for 12 months were compared to those who died, via a Welch's two sampled t-test.

I then compared the behaviour of rehabilitant and wild populations, by calculating a single overall mean activity budget per Age-sex class, per site. For TNBBBR and Batikap, the 0-3 month adaptation period was eliminated in order to show standardised, stable behaviour, and only nest-to-nest follows were used, therefore values for flanged males in TNBBBR are absent due to lack of data (Figure 2.6 and 2.7). Data for comparison to wild sites are presented as mean activity budget per Age-sex class, expressed as minutes of a 12-hour day, to be comparable to previous analyses from Morrogh-Bernard *et al* (2009)[44]. For comparison to other reintroduction sites, activities are calculated as the percentage of total follow time, adapted from Russon (2009)[11].

2.3.3.2. Sociality

To evaluate frequency and size of social aggregations, orangutan research typically records 'party' size[107,124,125], as the total number of independent individuals (excluding dependent offspring) within a 50-meter range of the focal. A party size of one therefore indicates a completely solitary individual. To investigate temporal changes in party size, I calculated a monthly mean party size per individual in TNBBBR to account for interindividual differences, and then separated them into age-sex classes in order to identify differences between sexes. Sociality data were unavailable for Batikap at the time of analysis. Reliability of data decreases as sample size decreases across time due to dispersal of individuals from the study site, therefore analyses were limited to 12 months post-release. Data from only the first two months post-release were collected for flanged males in TNBBBR, limiting analyses for this Age-sex class. Further, to confirm stability of sociality across time, I used Generalised Linear Mixed Models to fit a Poisson distribution using the log-link function to determine the effect of month-post release on party size. Data consisted of the party size recorded at each five-minute interval throughout the focal follow, for the 0-3 month period then the 4-12 month period separately. Age-sex class, individual, and follow number were implemented as random effects to account for repeated measures.

Mean activity budgets per time period (0-3 months and 4-12 months), were created for 16 individuals with data throughout this time, to determine whether each social activity occurred consistently across both time periods. Only follows >6 hours in length were used to increase reliability and generalisability with the small sample size. Normality of data and therefore violations of the model assumptions were checked via Shapiro-Wilk's tests, consequently paired t-tests were used if data were parametric, and Wilcoxon Signed Rank Tests were used if data were non-parametric, to compare between time periods.

To investigate dyadic interactions between the Age-sex classes, the focal and each associate, from each follow were paired (n=409), and Chi-Squared goodness-of-fit tests were used to determine whether interactions between each Age-sex class combination were more or less likely to occur than expected by chance. To investigate whether individuals associated with known individuals whom they progressed through

rehabilitation with, or nearby individuals from the same release group, stacked bar-plots were presented for visual comparisons.

To compare the sociality of reintroduced orangutans to wild orangutan, the mean party size of individuals in TNBBBR was displayed to compare to that of wild populations, also including information on sub-species, forest type, and population density. Standardised population density estimates were used, accounting for methodological differences in data collection, such as nest counts or animal counts, as well as nest decay rates, in order for more robust comparisons between sites[39].

2.3.3.3. Diet

Dietary data were collected during instantaneous sampling of behaviour at five-minute intervals. Activity (feeding or co-feeding) was recorded, followed by food type, and part of food consumed, then species (See Appendix D). Food items were recognised by field assistants and identified using local Dayak names, as binomial nomenclature is not yet available for all items. Samples of unknown food items were taken to basecamp for further identification. Different names relating to distinct parts of the same plant were combined wherever possible, to reduce the chance of species overestimating. Analyses of daily diet consisted of only follows greater than 6 hours in length in order to be representative of the majority of the active period, whilst maintaining an adequate sample size. Data from TNBBBR consisted of 461 follows, ranging from 6.1 to 13.3 hours (mean = 8.6 ±0.1 SE), and data from Batikap consisted of 795 follows, ranging between 6.1 and 13.2 hours in length (mean = 8.4 ±0.07 SE).

Food types were classified into the following classes, adapted from Rodman (2002)[126]; Fruit (Whole fruit, pulp, skin or seed, of both ripe and unripe fruit), Meristem (Meristematic tissue from palm and rattan), Pith (all material within plant stems, usually from Pandanus, grass or ginger), Bark (All bark material, cambium layer, or pith of branches), Leaf (Young and mature leaves, and leaf shoots), Invertebrate (Usually ants and termites), Epiphyte (Such as orchids and ferns), Other (Flowers, honey, rotten wood, fungi, sap, soil and water). For these analyses, all non-fruit food types are classified as ‘fall-back’ foods. To investigate longitudinal trends in dietary composition, the mean percentage of each food type was calculated per month post-release to investigate dietary changes across time, and the influence of rehabilitation.

Then, mean percentage of each food type were calculated per month of the year to compare against seasonality and subsequent fruit availability.

For comparing dietary composition between rehabilitant and wild populations, only full day nest-to-nest follows from TNBBBR and Batikap were used to standardise dietary composition across a total active period. Mean values (median values used at Tanjung Putting reintroduction site) were presented to provide an overall picture of dietary composition per site. To account for methodological differences in classification of food types between sites, only fruit, leaf, bark and invertebrate food types were classified, with all remaining items grouped into 'Other'.

2.4. RESULTS

2.4.1. Activity budgets

2.4.1.1. Longitudinal analyses of activity budgets

The percentage of time spent feeding significantly differed across trimesters in TNBBBR (Likelihood Ratio Test: $\chi^2_5=68.018$, $p<0.001$) and in Batikap ($\chi^2_{22}=111.39$, $p<0.001$) (Figure 2.1). Across both sites Tukey post-hoc tests revealed that time spent feeding was significantly lower in only the first trimester when compared to the subsequent trimesters. Trimesters two to six were not significantly different from each other signifying stability over time (Mixed model results table: See Appendix E).

Analyses of the percentage of time spent resting and travelling revealed similar trends (Figure 2.1), whereby both significantly differed across trimesters (Resting; TNBBBR: $\chi^2_5=51.282$, $p<0.001$, Batikap: $\chi^2_{22}=76.856$, $p<0.001$. Travelling; TNBBBR: $\chi^2_5=31.707$, $p<0.001$, Batikap: $\chi^2_{22}=74.568$, $p<0.001$). Tukey post-hoc test results revealed that both resting and travelling levels were significantly higher in trimester one compared with the subsequent trimesters for both sites, hence, trimesters two to six did not significantly differ from one another. (Mixed model results table: See Appendix F and G).

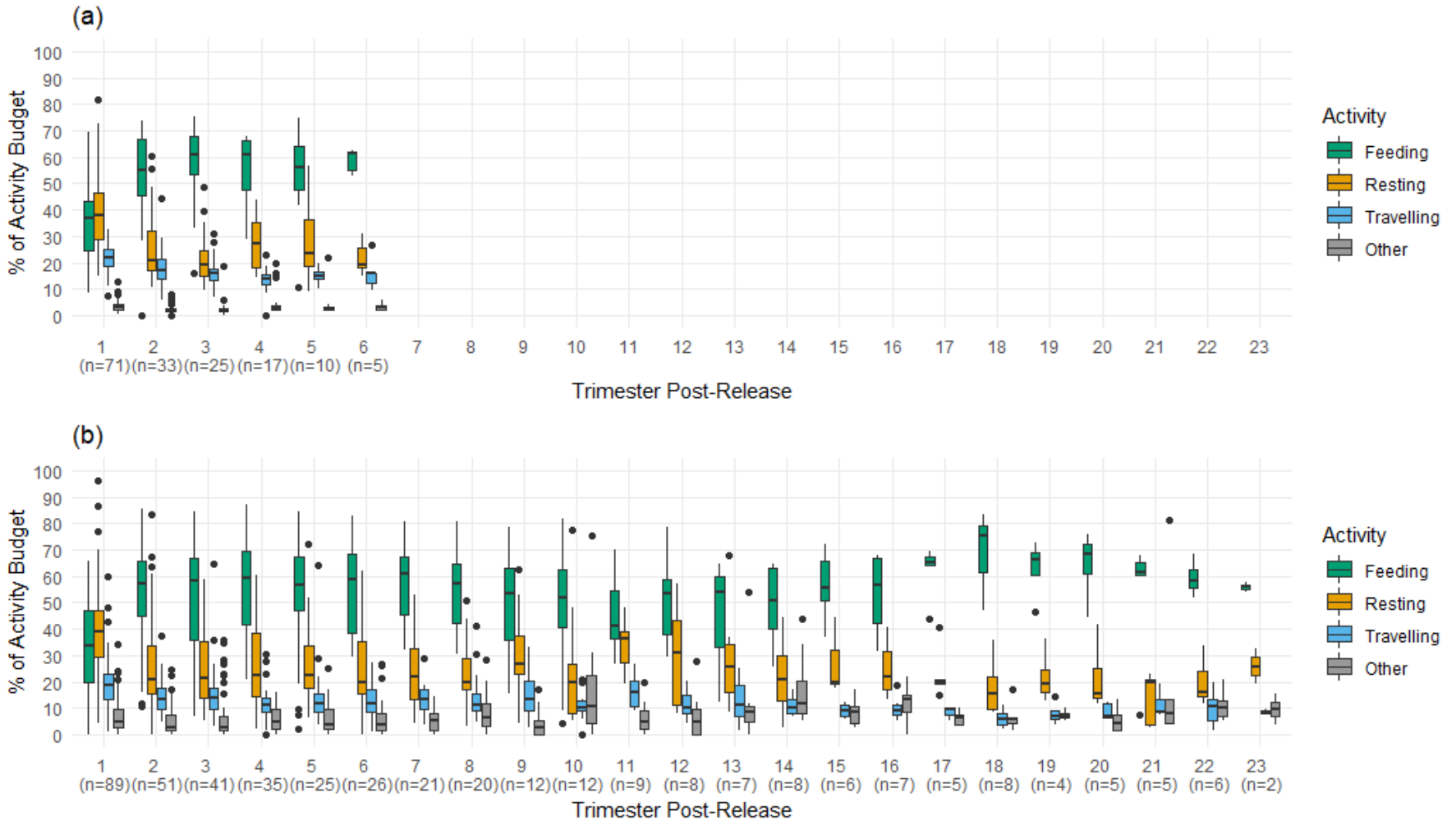

Figure 2.1. The percentage of time spent in each activity in (a) TNBBBR across 6 trimesters (18 months) post-release, and (b) Batikap, across 23 trimesters (5 years 9 months) post-release. The midline of the boxplot denotes the median value, whilst the upper and lower bound of the box correspond to the first and third quartiles. Lines extend up to 1.5*the interquartile range, with outlying data displayed as points. (n=number of individuals per Trimester)

2.4.1.2. Comparison between Age-sex classes

I found no significant difference between age-sex classes for time spent feeding (TNBBBR: χ^2_3=7.051, p=0.07, Batikap: χ^2_3=5.359, p=0.148), or travelling (TNBBBR: χ^2_3=0.259, p=0.967, Batikap: χ^2_3=6.034, p=0.11) (Figure 2.2). However, flanged males spent more time resting than the other age-sex classes (TNBBBR; χ^2_3=7.939, p=0.047, Batikap; χ^2_3=17.341, p<0.001).

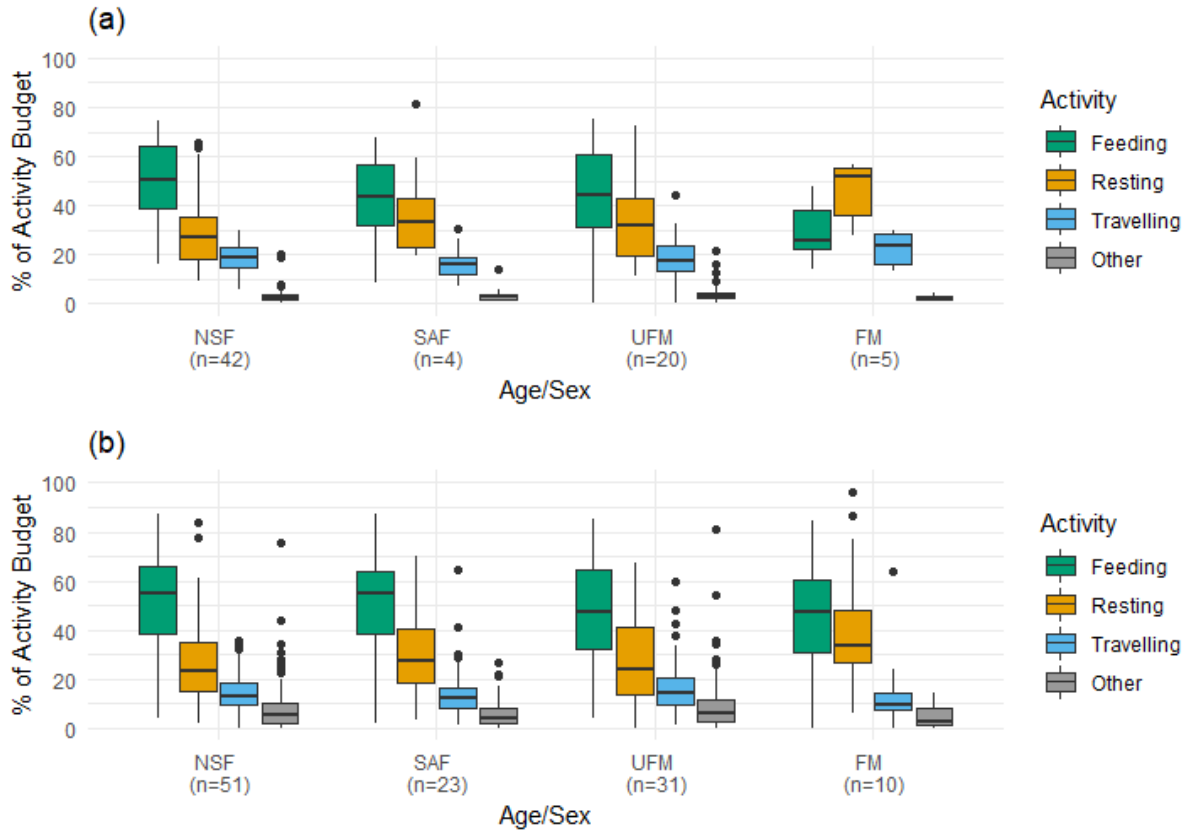

Figure 2.2. The percentage of time spent in each activity across each Age-sex class, for individuals in (a) TNBBBR and (b) Batikap. (NSF=Non-sexually active female, SAF= Sexually active female, UFM=Unflanged male, FM=Flanged male). The midline of the boxplot denotes the median value, whilst the upper and lower bound of the box correspond to the first and third quartiles. Lines extend up to 1.5*the interquartile range, with outlying data displayed as points. (n=number of individuals per Age-sex class)

2.4.1.3. Comparison between TNBBBR and Batikap

Across 4-12 months post-release, the mean percentage of time spent feeding in TNBBBR and Batikap was 55.9% (±1.33 SE) and 56.1% (±1.36 SE) respectively, and resting was 23.8% (±0.92 SE) and 24.4% (±1.13 SE) respectively, which were not

significantly different between sites (Feeding: T-test; t_{357}=0.057, p=0.9542, Resting: t_{366}=0.3677, p=0.7133). However, despite the same longitudinal trends found, the percentage of time spent travelling was significantly higher in TNBBBR (17.0% ±0.65 SE) when compared to Batikap (13.8% ±0.66 SE) (t_{355}=-3.4673, p<0.001). Focussing on feeding levels, subsequent analyses combine both reintroduction sites, TNBBBR and Batikap, to increase sample sizes.

2.4.1.4. Comparison of feeding levels per early life origin

The majority of individuals rescued are wild-born orphans (n=129), who have limited survival skills due to the loss of their mother, therefore must progress through rehabilitation to acquire independence and survival skills before being reintroduced into the wild. Other rescued individuals are either *fully-wild* individuals, adults rescued from areas under threat from deforestation, then taken to Nyaru Menteng for medical treatment, or *semi-wild* individuals, who, despite encountering humans and undergoing captive environments, have retained sufficient natural behaviours, such as an aversion to humans, and skills necessary for independent survival, such as foraging on wild food sources (n=39). Both *fully-wild* and *semi-wild* individuals were grouped together as 'Semi-wild' for these analyses, due to not requiring forest schools for skill acquisition. Finally, some individuals were born on pre-release islands (n=11), therefore are reintroduced alongside their rehabilitant mothers, then develop independence in the wild. Overall, feeding levels did not differ between the origin sub-groups (LRT, χ^2_2=1.536, p=0.464) (Figure 2.3).

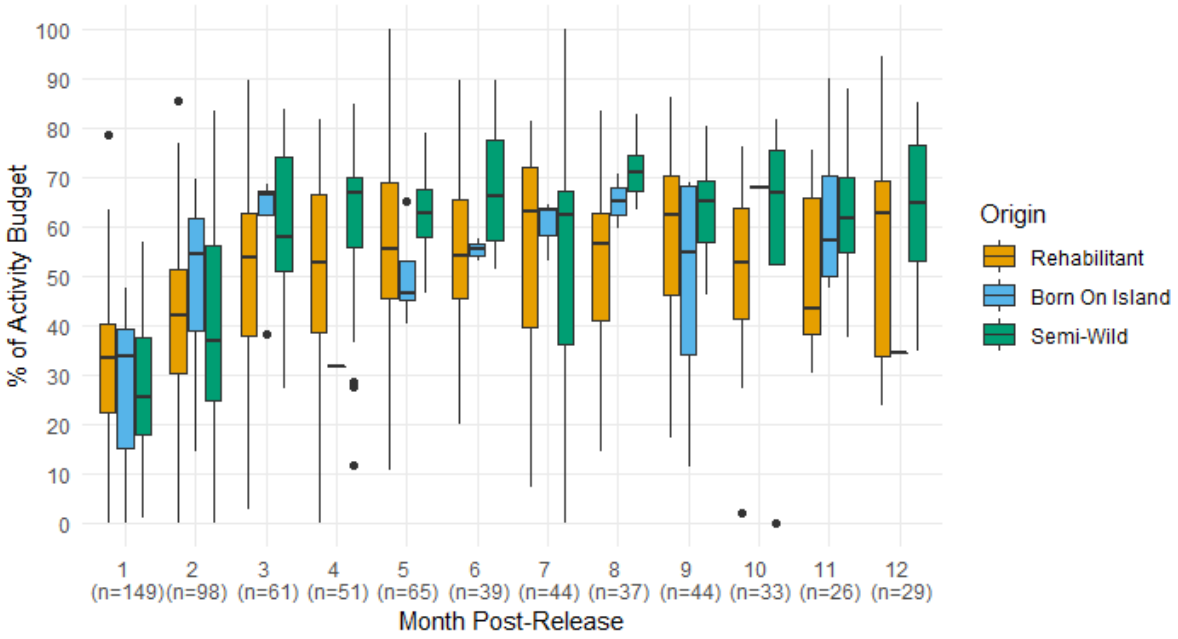

Figure 2.3. Feeding level per early life origin for all individuals in TNBBBR and Batikap combined, across 12 months post-release. The midline of the boxplot denotes the median value, whilst the upper and lower bound of the box correspond to the first and third quartiles. Lines extend up to 1.5*the interquartile range, with outlying data displayed as points. (n= total no. of individuals per month post-release)

2.4.1.5. Comparison of feeding levels per age at rescue

Focussing on rehabilitants, the majority of individuals rescued are between two and five years old (n=61), followed by those rescued under two years old (n=53). Those rescued over five years old (n=15) and are generally too mature to attend forest schools, therefore lack key learning opportunities. Those rescued over five years old generally spent less time feeding than those rescued under five years old, however this was not found to be statistically significant (χ^2_2=0.974, p=0.615), possibly due to small sample size (Figure 2.4).

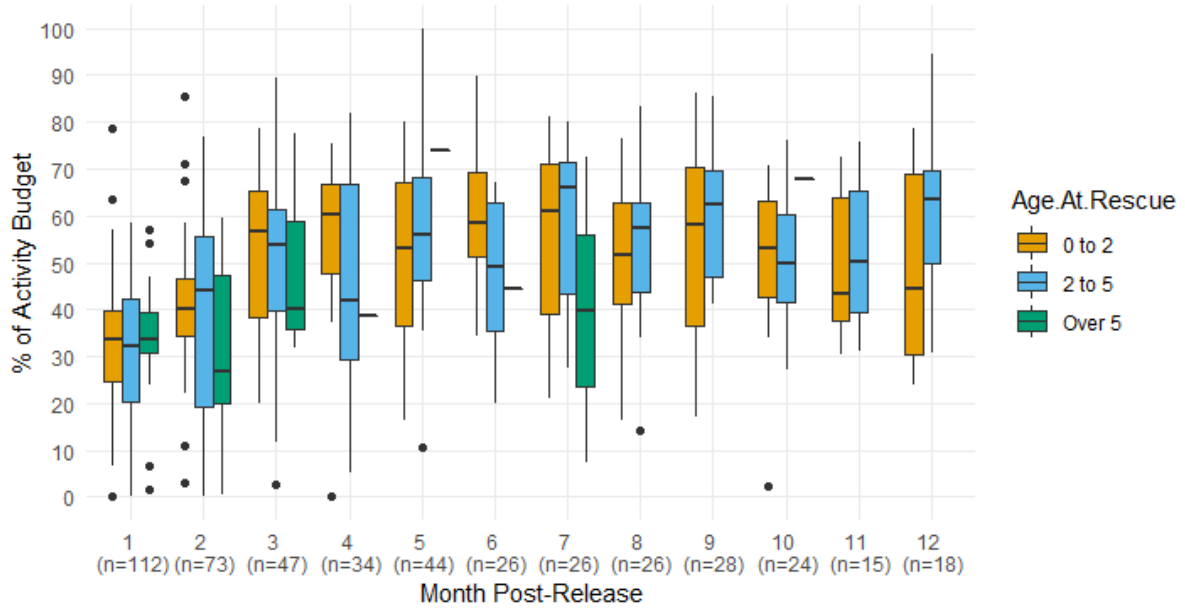

Figure 2.4. Feeding levels per age at rescue, for all rehabilitant individuals in TNBBBR and Batikap combined. The midline of the boxplot denotes the median value, whilst the upper and lower bound of the box correspond to the first and third quartiles. Lines extend up to 1.5*the interquartile range, with outlying data displayed as points. (n=total number of individuals per month post-release)

2.4.1.6. Comparison of feeding levels per outcome after 12 months

Nine independent individuals (and three dependent infants) were recorded to have died within the first 12 months post-release, presumed to be attributed to a failure to adapt, all of which were rehabilitant individuals. To confirm the effects of feeding level on survival rates, data from eight individuals that failed to survive 12 months post-release were compared to 53 rehabilitant individuals who were confirmed to have successfully survived independently. Individuals with insufficient data to confirm an outcome were not used in this analysis. Overall, successful individuals spent more time feeding (mean=48.6% ±2.98 SE) than unsuccessful individuals (mean=36.9% ±3.09 SE) (Welch's Two-sample t-test: t_{45}=-3.526, p<0.001) (Figure 2.5).

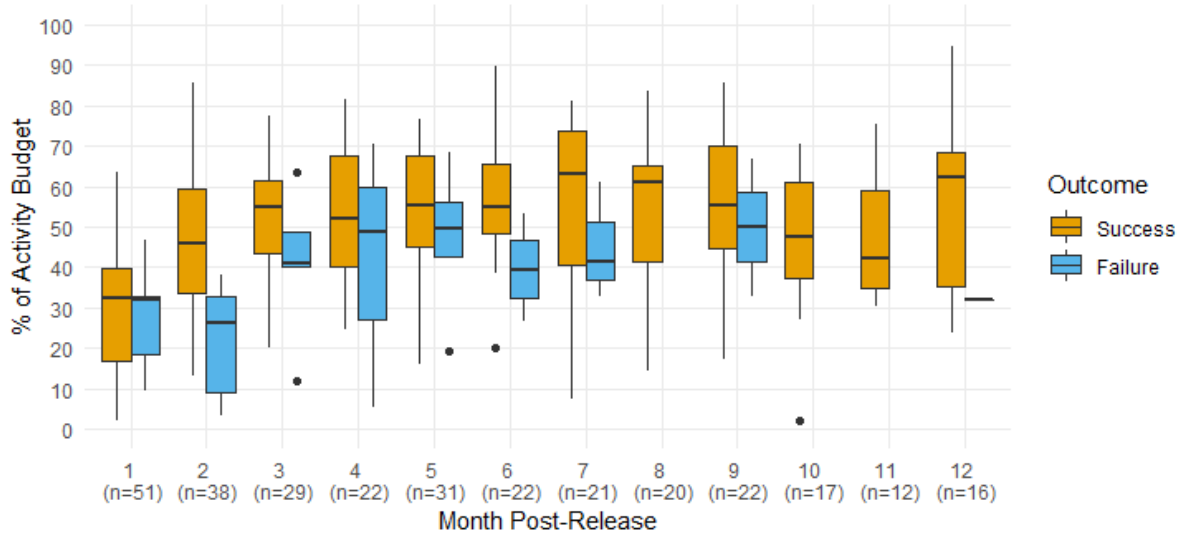

Figure 2.5. Feeding levels per outcome after 12 months post-release of rehabilitants in TNBBBR and Batikap combined. The midline of the boxplot denotes the median value, whilst the upper and lower bound of the box correspond to the first and third quartiles. Lines extend up to 1.5*the interquartile range, with outlying data displayed as points. (n=total number of individuals per month post-release)

2.4.1.7. Comparison of activity budgets between reintroduced and wild orangutans

Data are presented for the average activity budgets of each Age-sex class at TNBBBR and Batikap, compared to different wild sites (Figure 2.6) and other reintroduction sites (Figure 2.7). Overall, activity budgets for individuals in TNBBBR and Batikap fall within the ranges of those calculated for wild populations, and no substantial differences are visible, therefore can be considered comparable. Comparisons to other rehabilitant populations suggest that individuals in TNBBBR and Batikap are comparable to those in Sungai Wain, a previous BOS reintroduction site, and have adapted more successfully than individuals in sites such as Bukit Lawang, in which individuals are substantially effected by tourism and provisioning[82].

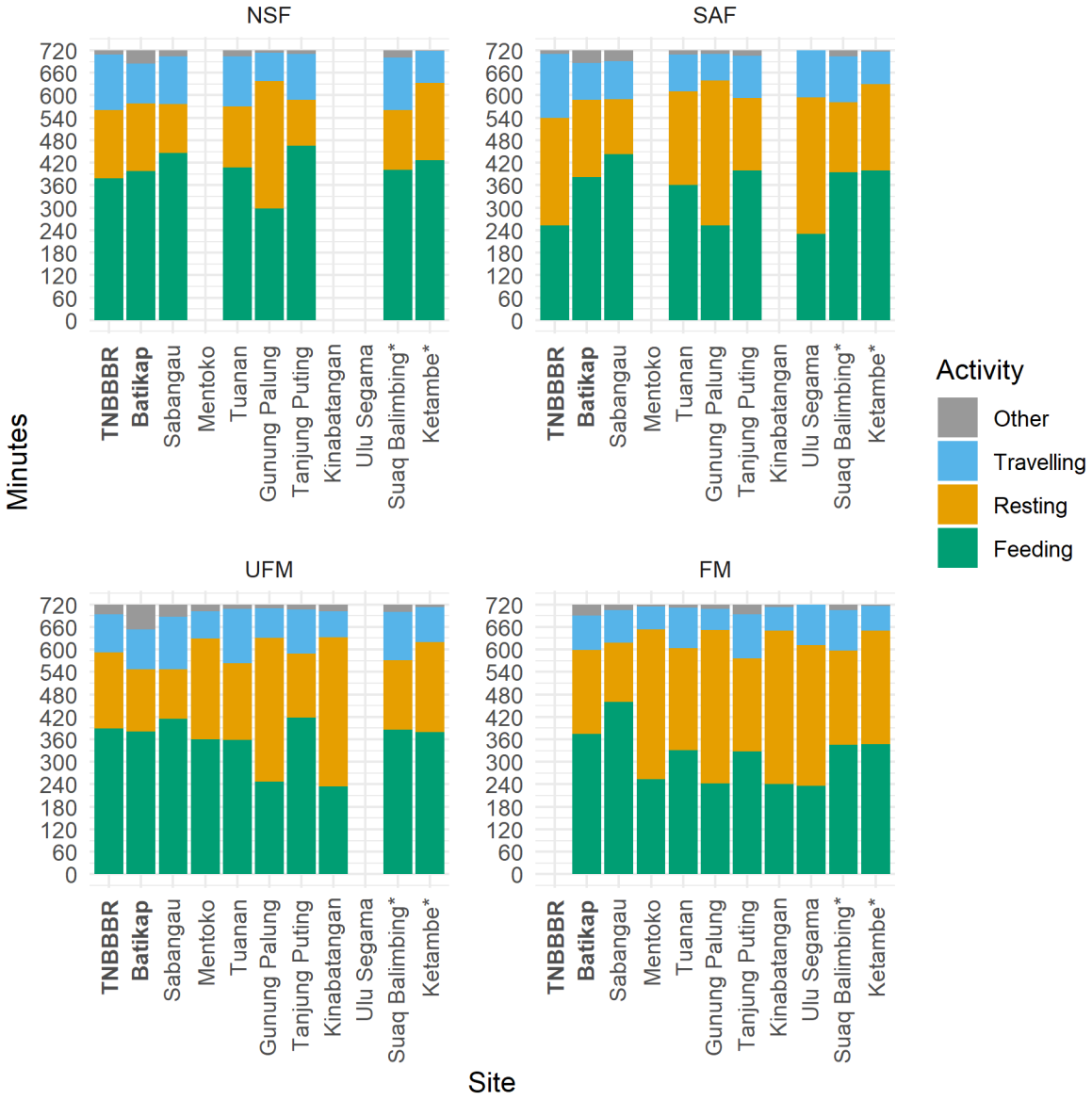

Figure 2.6. Mean activity budgets of non-sexually active females (NSF), sexually active females (SAF), unflanged males (UFM), and flanged males (FM), at TNBBBR, Batikap and different wild sites, expressed as minutes of a 12-hour day, adapted from Morrogh-Bernard (2009)[44].

Sources: Sabangau: Morrogh-Bernard (2009)[44],Mentoko: Mitani (1989)[127],Tuanan: Morrogh-Bernard (2009)[44], Gunung Palung: Morrogh-Bernard (2009)[44], Tanjung Puting: Galdikas (1988)[47], Kinabatangan: Morrogh-Bernard (2009)[44], Ulu Segama: MacKinnon (1974)[128], Suaq Balimbing: Fox (2004)[129] , Ketambe: Morrogh-Bernard (2009)[44].

*Sumatran site

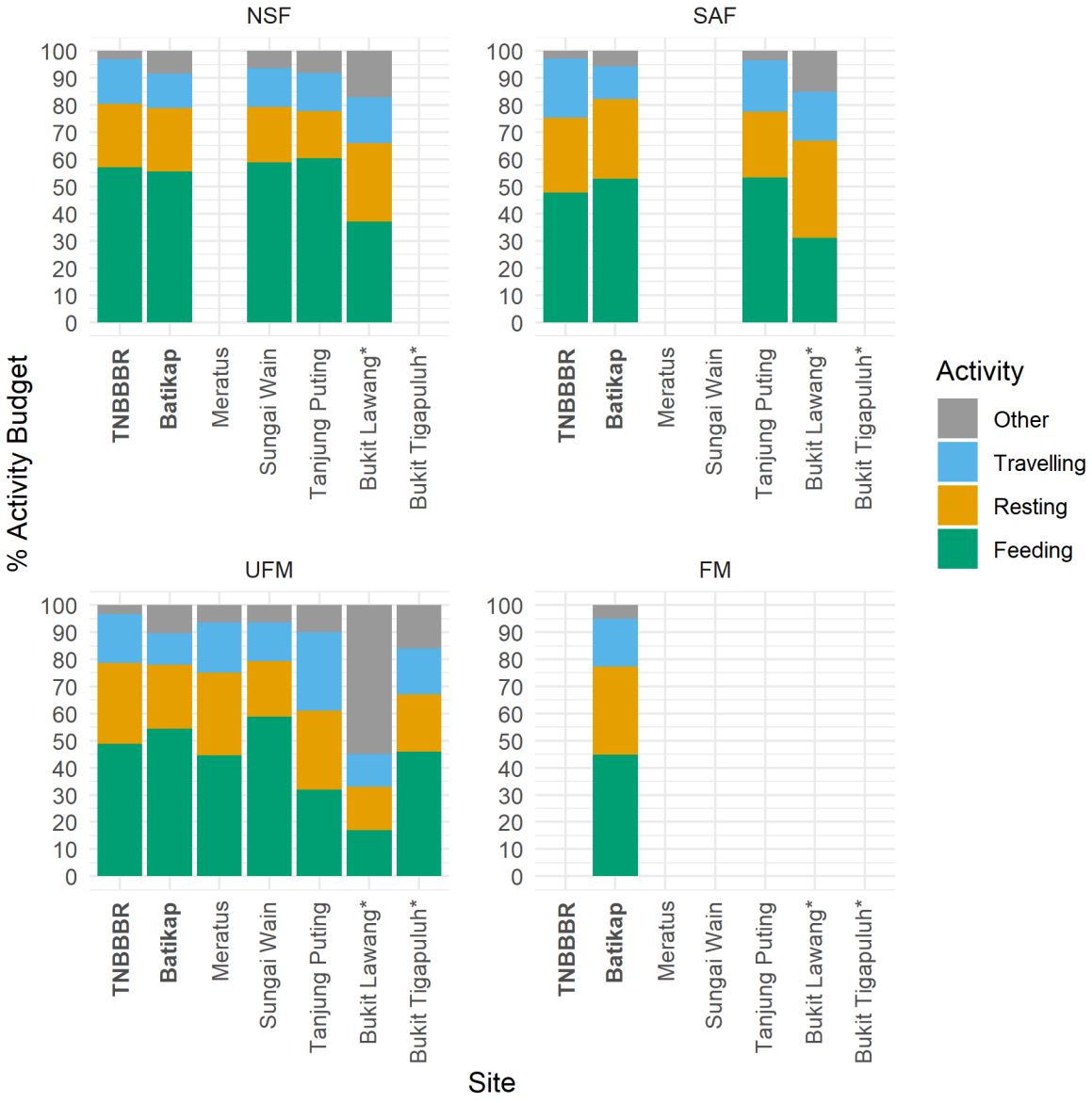

Figure 2.7. Mean activity budgets of non-sexually active females (NSF), sexually active females (SAF), unflanged males (UFM), and flanged males (FM), at different reintroduction sites, expressed % of total follow length, adapted from Russon (2009)[11].
Sources: Meratus: Grundmann (2006)[130], Sungai Wain: Fredriksson (1995)[75], Tanjung Puting: Snaith (1999)[80], Bukit Lawang: Dellatore (2007)[131], Bukit Tigapuluh: Russon (2009)[11]
*Sumatran site

2.4.2. Sociality

2.4.2.1. Party size

In TNBBBR party sizes were initially relatively large for all age-sex classes attributable to groups of individuals released together followed by a decrease over time whereby individuals disperse, until stabilisation occurs (Figure 2.8). Up to six individuals were recorded in association around the time of release, however most associations contain just two individuals. From three months onwards, a time-frame consistent with the 3-month behavioural adaptation period seen in activity budget analyses, mean party size of individuals in TNBBBR stabilises at approximately 1.1.

The results of Generalised Linear Mixed Models support the notion that overall, party size decreases and becomes more stable over time as depicted by the slope of the regression lines (Figure 2.8) (0-3 months; GLMM, z_{35426}=-8.028 ± SE 0.033, $p<0.001$, 4-12 months; GLMM, z_{24831}=-0.770 ± SE 0.005, $p=0.442$) (Mixed model results table: See Appendix H)

On average, Orangutans in TNBBBR were solitary 56.7% of their time during the three months following reintroduction, increasing to 90.3% of the time during the stabilised period between 4-12 months post-release. Sexually active, parous females (SAF) were the most solitary class, spending 99.6% of their time alone or just with their infant during the 4-12 month period, whilst unflanged males were the most gregarious class, spending 64% of their time in association. Flanged males were excluded from the 4-12-month analysis due to only having data from the first two months post-release.

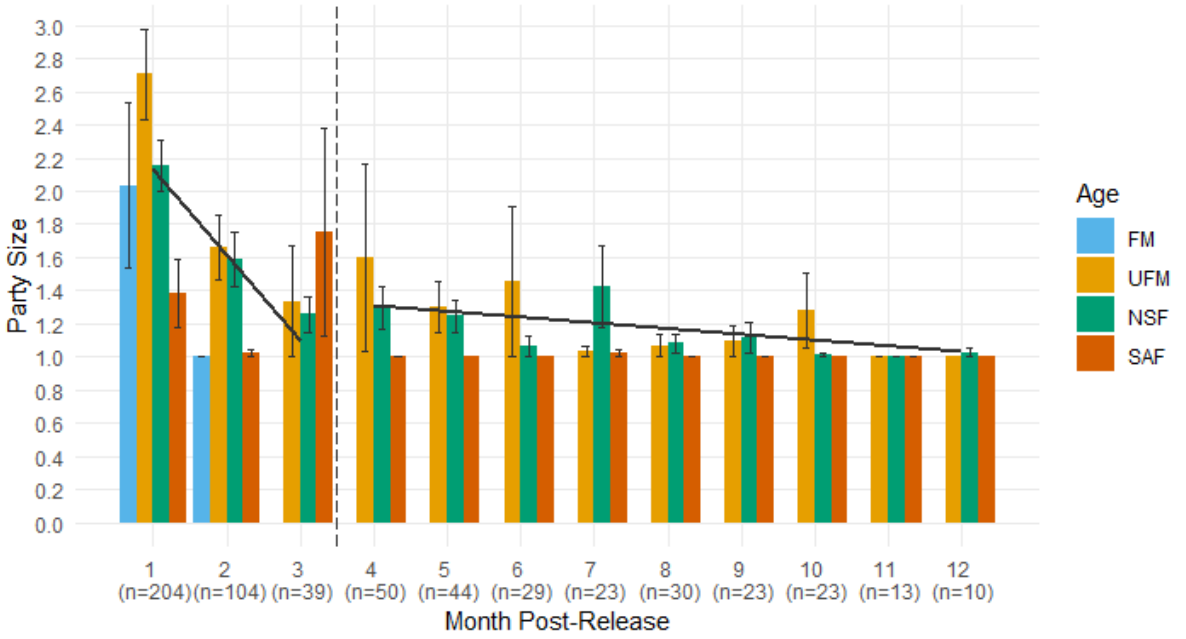

Figure 2.8. Mean party size of flanged males (FM), unflanged males (UFM), sexually active females (SAF), non-sexually active females (NSF) across months post-release in TNBBBR ± standard error. Vertical line separates the adaptation period from stable, standardised period. Regression lines fit separately for 0-3 month and 4-12 month periods. (n=total number of follows).

2.4.2.2. Social activities

For orangutans classified as being part of a social party, results reveal that resting and travelling were the most observed activities during the 0-3 month adaptation period (Figure 2.9), significantly higher than when observed during the 4-12 month (Resting; V_{15}=136, p<0.001, Travelling; t_{15}=3.1982 p<0.01). Whereas, feeding and co-feeding were the most observed activities during the 4-12 month period, with co-feeding recorded significantly more often (Co-feeding; t_{15}=-4.7173 p<0.001). Time spent nest building did not significantly differ between the time periods (t_{15}=1.24, p=0.234), confirming that individuals consistently spent approximately 10 minutes building nests. Social interactions with other orangutans such as mating (n=14) and conflict (n=4) were rare and only occurred during the adaptation period for the individuals sampled therefore restricting comparative statistical analyses. Interactions with observers (IWO) was only recorded for two individuals during the 4-12 month period, again preventing statistical analyses. However, the rarity of social behaviours seen after the adaptation period further reinforces that individuals associate for food resources and not physical interaction with conspecifics during this time.

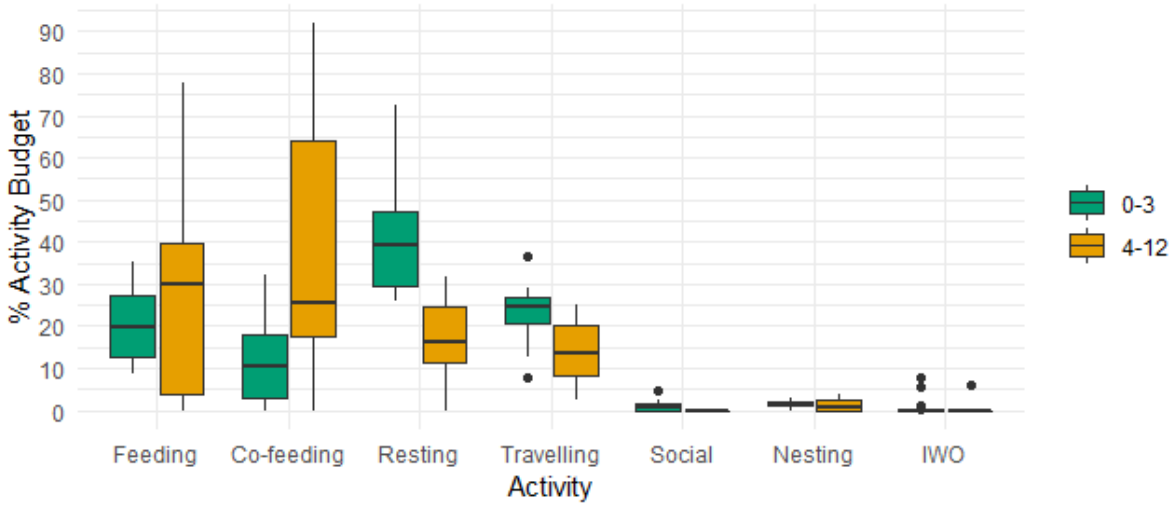

Figure 2.9. Activity budget whilst in party, during the 0-3 and 4-12 month periods. The midline of the boxplot denotes the median value, whilst the upper and lower bound of the box correspond to the first and third quartiles. Lines extend up to 1.5*the interquartile range, with outlying data displayed as points.

2.4.2.3. Dyadic interactions

The focal and each associate were paired to further investigate whether members of each age-sex class showed preference for an associate of a particular age-sex class. Results revealed that the most common interactions were between non-sexually active females and unflanged males (43.3%), followed by non-sexually active females together (33.5%) (Table 2.1). Chi-squared goodness-of-fit tests were calculated to determine whether dyadic interactions were equal to those expected by chance, accounting for the number of individuals in each Age-sex class and increase in number of individuals with each new release. Overall, individuals associated least with sexually active females and flanged males, values of which were consistently lower than expected by chance, implying active avoidance. Non-sexually active females and unflanged males interacted with each other the most frequently, with the number of interactions being consistently higher than expected by chance. No interactions were recorded between flanged males, which was significantly lower than expected by chance. The expected Chi-Squared values assume equal possibility of encountering each individual, therefore limitations exist whereby some individuals may have dispersed further from the focal than is possible to travel in one day, hence less likely

to associate. However, the majority of interactions occurred within the first month post-release, whereby individuals are likely to be within range of association.

Table 2.1. The percentage of time each Age-sex dyad combination was observed. Chi-Squared statistic, with observed values higher or lower than expected by chance.

	FM	**UFM**	**NSF**	**SAF**
FM	0% **Lower** X^2_7=1.73, p<0.05*			
UFM	1.2% **Lower** X^2_7=9.61, p>0.05	8.1% **Higher** X^2_7=45.51, p>0.05		
NSF	5.4% **Lower** X^2_7=10.93, p>0.05	43.3% **Higher** X^2_7=44.17, p>0.05	33.5% **Higher** X^2_7=22.66, p>0.05	
SAF	0.5% **Lower** X^2_7=4.99, p>0.05	3.9% **Lower** X^2_7=18.55, p>0.05	3.9% **Lower** X^2_7=35.26, p>0.05	0.2% **Lower** X^2_7=4.81, p>0.05

Individuals were reintroduced in eight separate release groups throughout the study in TNBBBR, whereby individuals spent the final process of rehabilitation on Kaja pre-release island (n=44), Bangamat pre-release island (n=25), partner rescue centre Samboja Lestari (n=1), or were translocated from the wild (n=2). The majority of interactions occurred within the first month post-release as groups of individuals released together stayed within range of association until dispersal, hence most interactions during this time were between individuals from the same release group (Figure 2.10). Over time, as the number of interactions decreased, the few individuals that chose to interact mostly associated with familiar conspecifics from the same pre-release island, and rarely with individuals from the same release group.

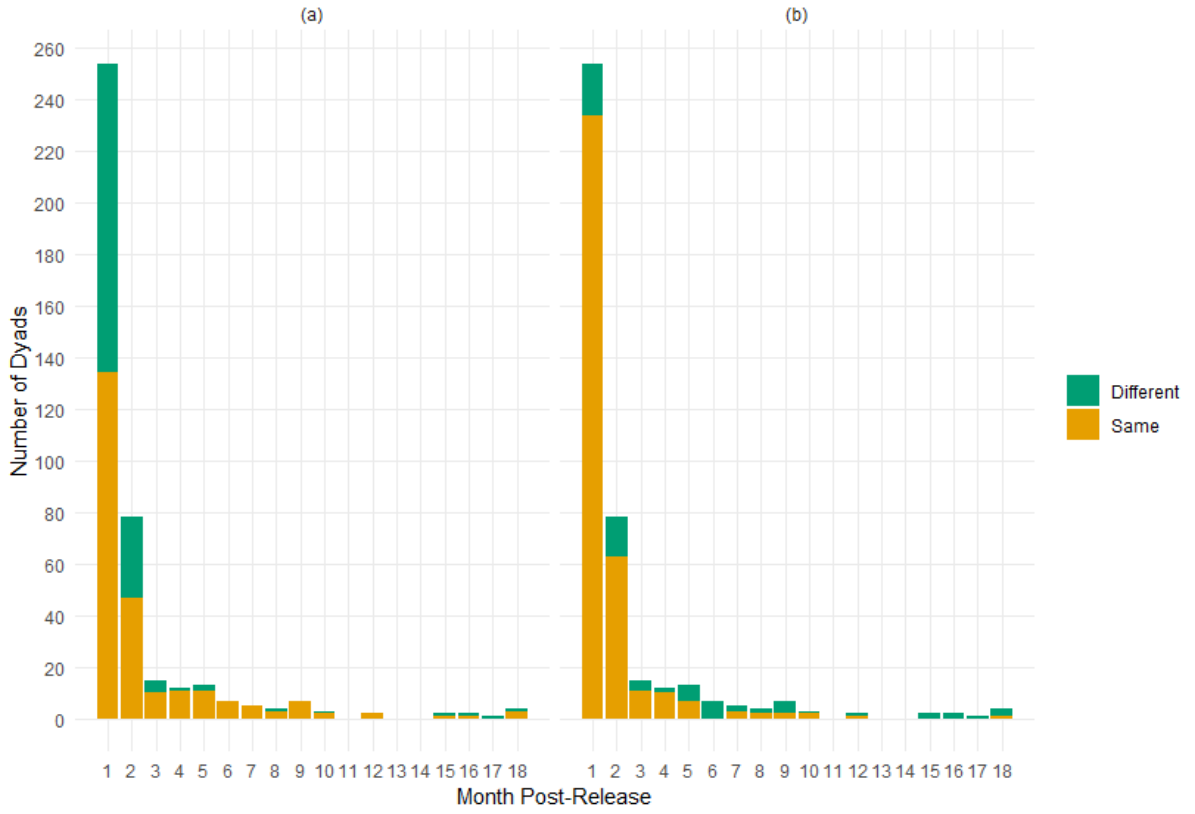

Figure 2.10. Number of dyadic interactions containing members of (a) the same or different pre-release environment, and (b) same or different release group.

2.4.2.4. Comparison of sociality between reintroduced and wild orangutans

Trends are seen between islands, whereby mean party size and often population density of wild populations are larger on Sumatra than Borneo (Table 2.2). Trends are also seen between forest types; whereby party size is higher within peat swamp forests than mixed dipterocarp forests. In terms of sub-species, and habitat type, orangutans in TNBBBR are most comparable to those in Gunung Palung, which also have a similar mean adult female party size, concluding that the mean party size of reintroduced orangutans in TNBBBR is similar to comparable wild populations.

Table 2.2. Mean adult female party size and population density (measured in individuals per square kilometre) of wild orangutan populations on Borneo and Sumatra. LD=Lowland mixed dipterocarp forest, PS= Peat swamp forest. Kutai, Tanjung Puting, Tuanan and Sabangau contain disturbed forests.
Superscripts refer to reference numbers for data sources.

Island	Site	Species	Forest type	Adult Female Party Size	Density (ind km^{-2})
Sumatra	Ketambe	*P. abelii*	LD	1.5[107]	3.05[39]
	Suaq Balimbing	*P. abelii*	PS	2.0[125]	7.2[39]
Borneo	Kutai	*P. p. morio*	LD	1.3[49]	3.66[132]
	Gunung Palung	*P. p. wurmbii*	LD (main) + PS	1.05[49]	3.41[39]
	Tanjung Puting	*P. p. wurmbii*	PS (main) + LD	1.2[133]	2.72[39]
	Tuanan	*P. p. wurmbii*	PS	1.35[106]	3.84[39]
	Sabangau	*P. p. wurmbii*	PS	1.2[134]	1.93[39]
	TNBBBR	***P. p. wurmbii***	**LD**	**1.1**	

2.4.3. Diet

2.4.3.1. Dietary repertoire

In TNBBBR, a total of 237 food items were identified by local Dayak names. Data on local names were unavailable for Batikap at the time of analyses. As it is likely that some food items are from distinct species, but display similar morphologies and are therefore given the same name, the number of food items recorded is likely an underestimate of the total number of species consumed. The total number of food items recorded increased rapidly during the first few months post-release, likely due to initial exploration of the habitat and food items. Overall, the number of species consumed per day varied from 1 to 20, with a mean of 7 species. All food items recorded were plant matter with the exception of ants, termites, wasps, honey and soil.

59 of these food items were eaten only once, by one individual, suggesting foraging by trial and error, whereas nearly all individuals were recorded eating invertebrates, epiphytes, figs, '*Kayas'*, '*Kacang dahan'*, and '*Pahakung'*.

2.4.3.2. Dietary composition

Dietary composition varied dramatically between follows, but overall, fruit was the most consumed food type, a higher quality food with high caloric content[135], followed by lower quality leaves, bark and meristematic tissue. In Batikap and TNBBBR the mean percentage of fruit consumed fluctuates substantially across time, whereby a decrease in fruit consumption is substituted by an increase in fall-back foods, particularly meristematic tissue. Overall, a slight increase in fruit consumption across months post-release is visible, however substantial variation exists between individuals and between months (Figure 2.11). Across time of the year, fruit consumption fluctuated between months and between years (Figure 2.12), likely in response to seasonality and subsequent fruit availability, however analyses of phenology are necessary to validate this hypothesis.

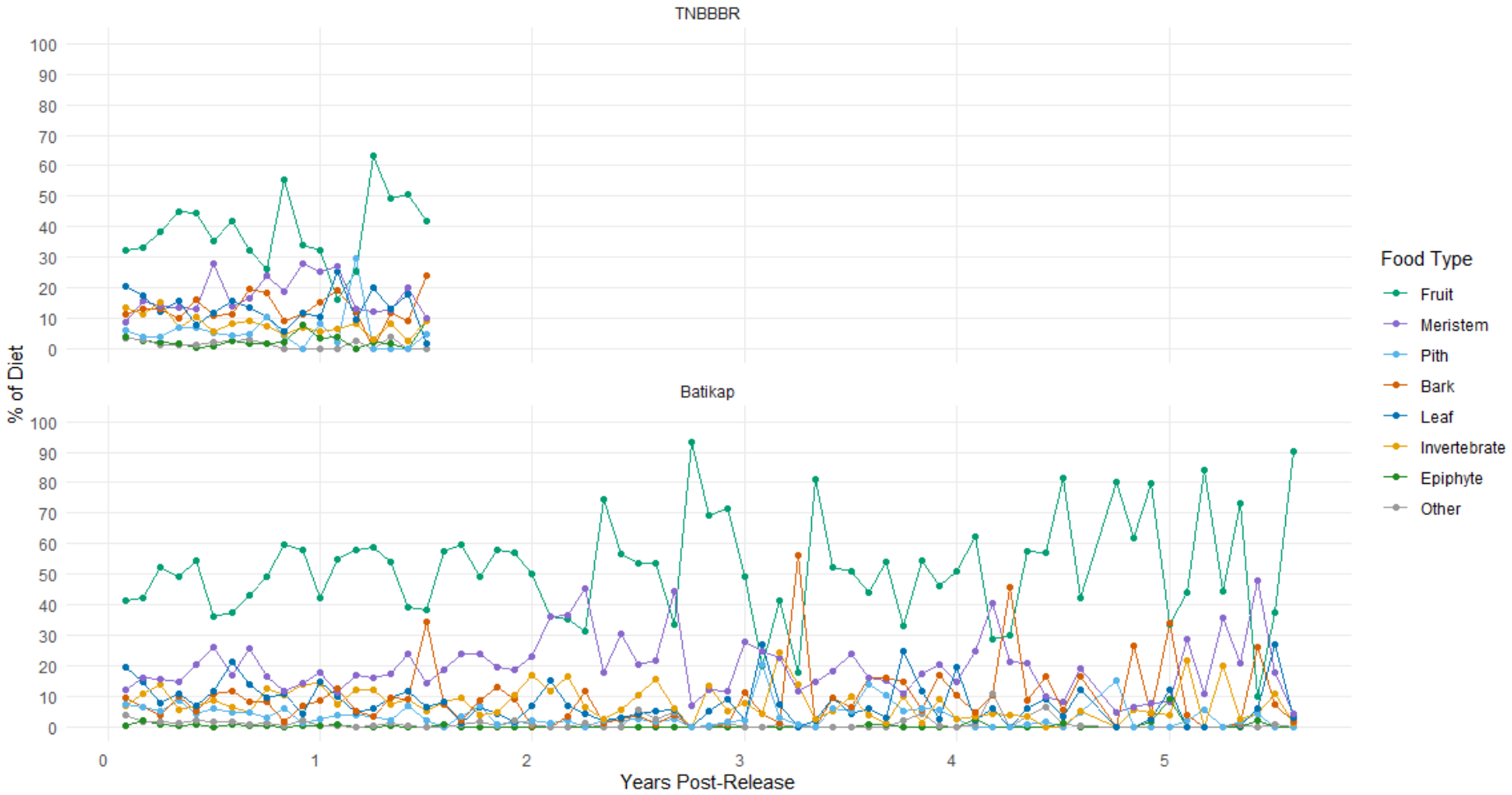

Figure 2.11. Mean dietary composition per month post-release, across 18 months for individuals in TNBBBR, and across 6 years for individuals in Batikap. (Using all follows >6 hours)

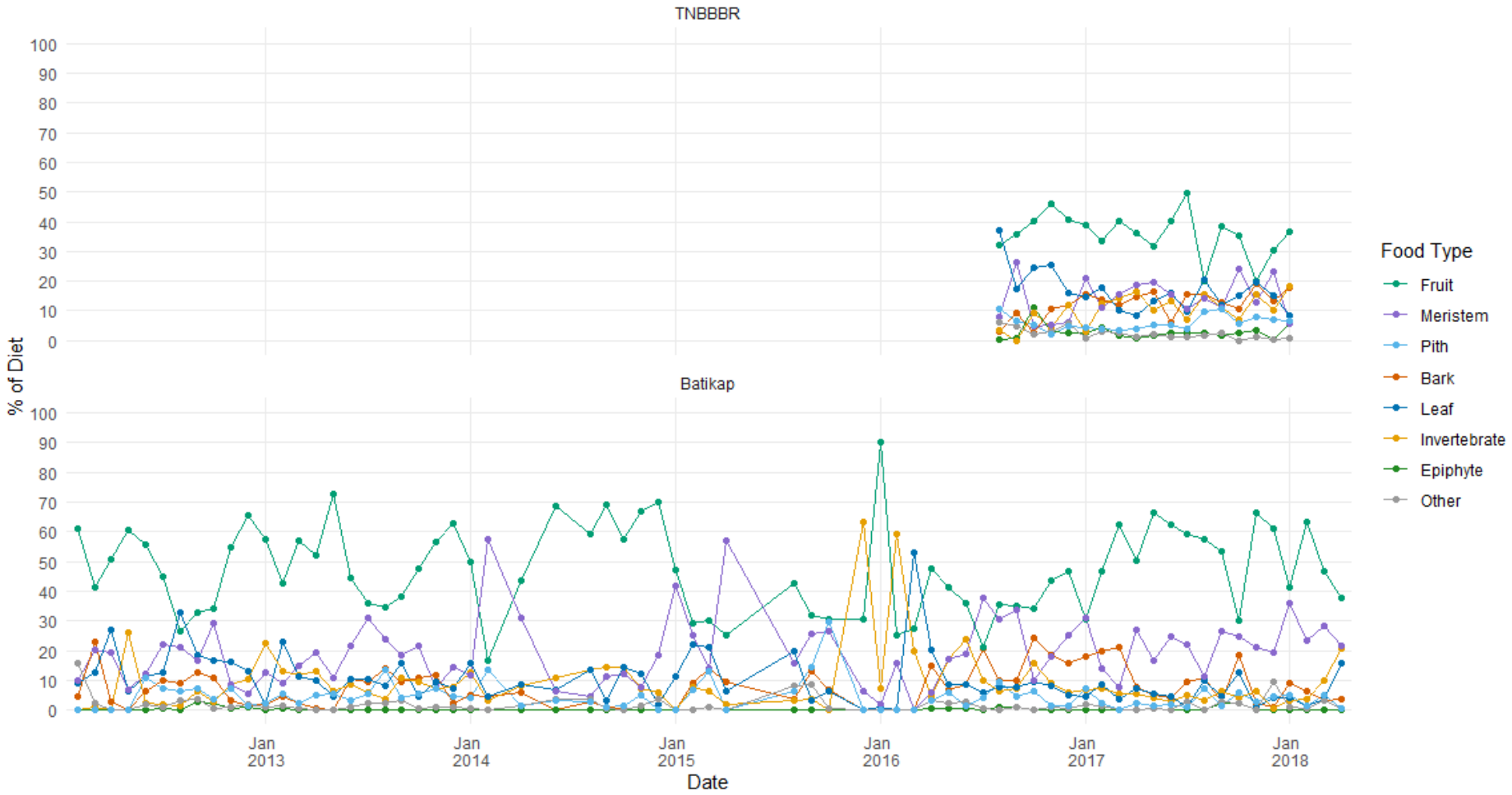

Figure 2.12. Mean dietary composition per month of the year, from February 2012 to April 2018 for individuals in Batikap and from August 2016 to January 2018 for individuals in TNBBBR. (Using all follows >6 hours)

2.4.3.3. Comparison of diet between reintroduced and wild orangutans

Amongst wild populations, fruit accounts for over 50% of the diet (Figure 2.13a), whereas amongst reintroduced populations, fruit consumption is often far less (Figure 2.13b). Individuals in TNBBBR and to a lesser extent, Batikap, consume a considerable proportion of 'Other' food types, primarily pith and meristem. The wild population in Gunung Palung serves as the most meaningful comparison due to being the same sub-species and similar habitat type, however mean fruit consumption in Gunung Palung (70%) is far greater than in TNBBBR (37%) and Batikap (52%). Overall, despite comparable activity budgets whereby individuals in TNBBBR and Batikap spend a similar amount of time feeding, fruit consumption is lower than wild populations in comparable habitats, implying reintroduced individuals rely on other food types to maintain sufficient nutrition.

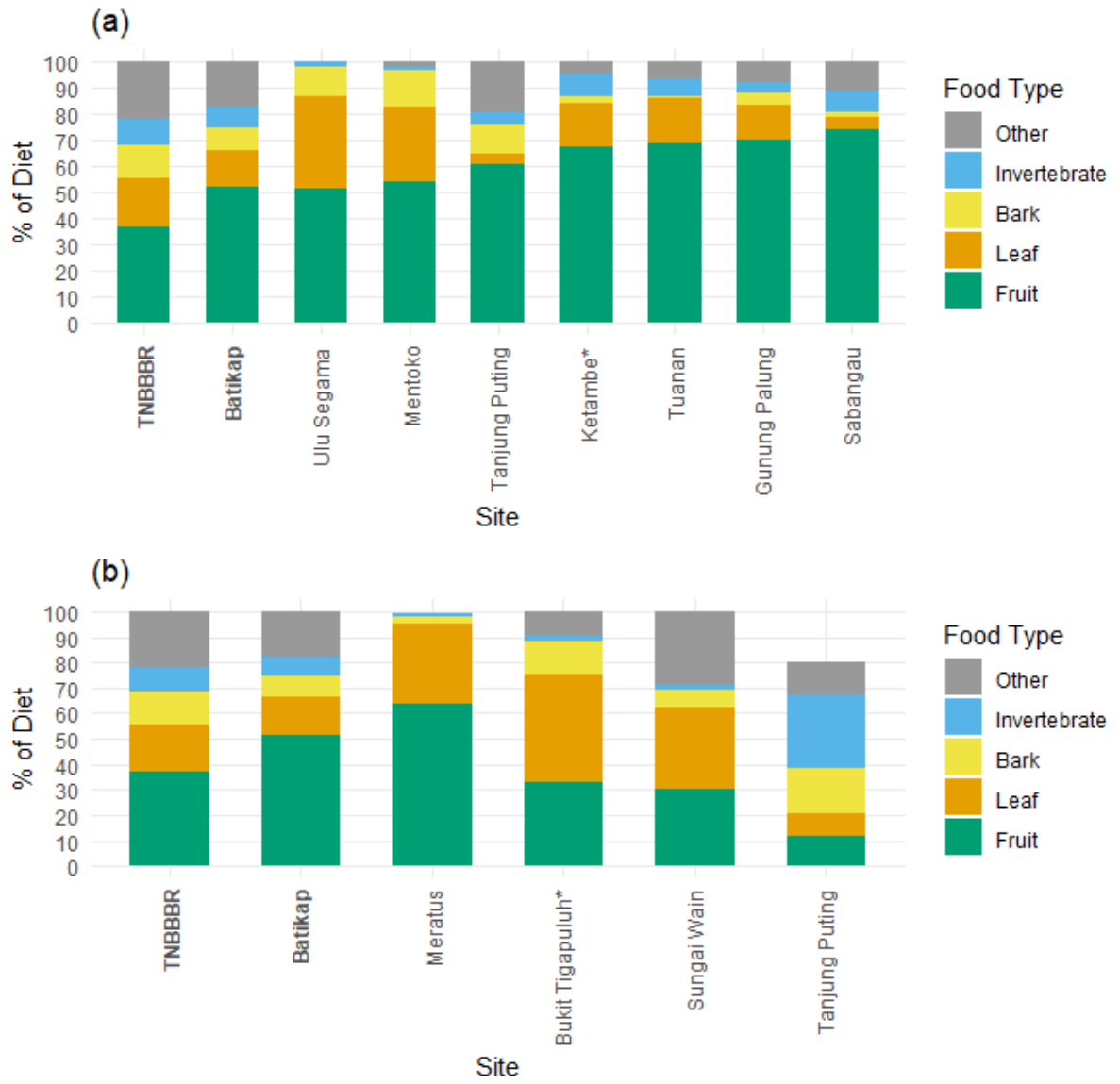

Figure 2.13. Dietary composition at TNBBBR and Batikap, compared to (a) wild sites, adapted from Morrogh-Bernard (2009)[44], and (b) other reintroduction sites, adapted from Russon (2009)[11]. Only nest to nest follows used for TNBBBR (n=139) and Batikap (n=165). Dietary composition expressed as a mean percentage of total feeding time for all sites except median used at Tanjung Puting reintroduction site.
*Sumatran site

2.5. DISCUSSION

The way in which orangutans allocate their time provides insights into habitat quality, seasonality and inter-individual differences[127]. For reintroduced orangutans, the variation in time allocated to particular activities across time post-release provides crucial insights into the extent of post-release ecological competence. Longitudinal

analyses of activity budget revealed that time spent exhibiting the three main activities; feeding, resting and travelling, was consistently different in the first trimester when compared to the subsequent trimesters. The subsequent trimesters did not significantly differ from one another signifying a level of stability was reached after the first three months. An adaptation period of approximately three months post-release was therefore identified, whereby individuals' behaviour rapidly changed in response to reintroduction, to manage the new, unfamiliar environment. These findings are similar to results from previous reintroductions by BOS into Sungai Wain, East Kalimantan, where newly released rehabilitants spent less time feeding and twice and much time resting when compared to more experienced rehabilitants[75], until behaviour began to stabilise at nine months post-release.

The initial lack of time spent feeding may be attributed to pre-release protocols, and potential post-release stress. Pre-release protocols involve, rehabilitation through 'forest school' and then semi-wild protected islands of forest termed 'pre-release islands', designed to mimic wild environments. Pre-release islands provide wild fruit trees and other food items available for individuals to forage on, but supplementary food is also given twice per day to ensure individuals consume the necessary nutritional requirements whilst learning to forage independently. Individuals must display independent foraging as a prerequisite for reintroduction, although many often also consume supplementary food due to ease and consistency, therefore are likely to expect food provisions upon release, resulting in a reduced foraging effort. Additionally, during the first day of reintroduction, a recovery period is expected due to anaesthesia prior to veterinary health checks and transportation, as well as elevated levels of stress in response to the unfamiliar environment, also likely contributing to the reluctancy to forage. Although nutritional value differs depending on the food source, time spent feeding provides a general indication of energy intake, assuming individuals seek to maximise foraging efficiency[129]. Overall, changes in foraging behaviour can substantially affect nutritional intake and energy balance[136]. Further, an initially low number of different food items recorded supports the notion that newly released individuals find and recognise fewer food sources than experienced individuals.

The initial reduction in foraging effort was compensated by elevated levels of resting and travelling, suggesting exploration of release site, in order to gain information on

the spatial distribution of food resources and neighbouring conspecifics[137], a key behaviour for home range establishment[138,139]. Furthermore, elevated levels of travelling can also imply more time spent searching for familiar food sources. Then, as individuals begin to try new, previously unencountered food sources, search time is likely to decrease, as feeding levels increase due to a broader dietary repertoire. The subsequent increase in time spent feeding implies individuals have learned food provisions are unavailable and therefore need to forage independently. Then, the maintenance of a stable level of feeding at 50-60%, across time suggests nutritional requirements are being met.

Studies of wild orangutans have revealed that activity budget differs as a function of age-sex class, as adult females, particularly those who had recently given birth, foraged less than adult males[127], and smaller sub-adult males travelled more and rested less than larger adult males. Further, unflanged males must actively search for receptive females, therefore elevated levels of travel are likely when compared to flanged males, who attract females[140]. Thus, social and ecological factors influence the manner to which individuals allocate their time. In TNBBBR and Batikap, feeding and travelling levels did not significantly differ as a function of age-sex class, however flanged males in TNBBBR rested significantly more than the other age-sex classes. Similar trends have been recorded in wild flanged males[44], attributed to the ecological constraints of large body size, socio-sexual strategies[141], together with a reduction in time spent travelling. Contrastingly, no significant difference was seen in flanged males in Batikap, suggesting results from TNBBBR may be an artefact of small sample size as data from only the first two months post release were available, skewing data towards the 0-3 month adaptation period.

The extent to which rehabilitation influences post-release behaviour, has rarely been studied. Post-release success may depend on both early-life experiences in the wild and time spent progressing through the various stages of rehabilitation. Individuals retaining knowledge of wild food sources, seasonal fluctuations in fruit availability and habitat heterogeneity will inevitable have higher rates of survival, when compared to rehabilitants lacking those experiences. However, analyses comparing the feeding levels of rehabilitants to those born on pre-release islands, and semi-wild individuals, reveals no significant differences, implying the BOS rehabilitation programme does not hinder time allocated to foraging. Further, individuals rescued over the age of five

suffer restricted early-life experiences due to substantial time spent in captive environments as part of the illegal pet trade, and subsequent absence from forest school. Despite this, there was no overall significant difference found between the feeding levels of individuals rescued at different age groups, implying an individual's history prior to rescue does not detrimentally affect post-release behaviour. However, the individuals who had been confirmed to have failed to survive 12 months post-release were all rehabilitants who progressed through forest schools and rehabilitation stages in order to learn key survival skills. Comparisons between the feeding levels of successful and unsuccessful individuals revealed, those who did not survive spent significantly less time feeding, suggesting foraging inadequacies influenced their outcome. Thus, increased monitoring of individuals who did not attend forest school is critical for ensuring sufficient foraging levels are exercised.

Inter and intra-site variation in wild orangutan activity budget exists, attributable to a host of interacting factors such as habitat type, habitat quality, fruit availability, seasonality and Age-sex class[129]. Statistical comparisons between TNBBBR and Batikap revealed similar activity budgets, suggesting longitudinal behavioural changes are a response to reintroduction, and not release site. Moreover, comparisons to published data show that the time allocated to feeding, resting and travelling, fell within the ranges of the activity budgets of comparable wild populations. Although limitations in data availability preclude formal statistical analyses, these comparisons provide reassuring evidence that reintroduced orangutans do not substantially differ in their behaviour compared to their full wild counterparts. Thus, the data presented here provide evidence for the success of reintroductions into TNBBBR and Batikap in regard to creating a population behaviourally comparable to wild orangutans.

Analyses of the social interactions of reintroduced orangutans is necessary to determine how early life experiences in rehabilitation, instead of natural associations with their mother, have influenced post-release social behaviour. Group living is initiated in nursey facilities, then continues throughout forest schools, socialisation cages and pre-release islands, thus rehabilitation is anticipated to increase sociality. Results revealed initial gregariousness around the time of release, attributable to groups of approximately six individuals released together, increasing the likelihood of being within range of association. Further, the elevated levels of resting recorded following release maintained a relatively high density of individuals, which provided

more opportunities for mating, but also elevated levels of aggression, likely due to social stress. During the 0-3 month adaptation period, aggregations were a combination of passive and social, whereby resting was the most common activity, which may have provided vital opportunities for social learning, followed by travelling which may have encouraged exploration of the unfamiliar environment. Over time, as individuals dispersed, sociality decreased then stabilised at a party size of approximately 1.1, as associations were primarily passive. Thus, reintroduction protocols temporarily increased sociality, but after three months post-release individuals consistently displayed relatively few social interactions.

Orangutans are capable of differentiating between conspecifics and recognising previous associates, necessary for distinguishing between relatives, non-relatives, dominant individuals and mates[142,143]. Due to no known relatedness between rehabilitants, no spatial patterns of relatedness were created upon release, but my data suggests that individuals show preference for associating with known individuals. Those from the same pre-release environment were more likely to associate than those from different pre-release environments once a stable level of sociality was reached. This result suggests rehabilitation protocols influence the social structure of a population, as social tolerance is greater towards known conspecifics, similar to the social tolerance exhibited by wild female relatives[108]. This finding is useful for planning release groups and predicting spatial distribution throughout the release site. Further, evidence presented suggests differences in sociality between age-sex classes, where non-sexually active females and unflanged males were the most social, and sexually active females and flanged males remained more solitary, similar behaviour seen in wild individuals[144]. Wild nulliparous females often associate with males for mating opportunities, or with females likely to share an attraction to the same male[106], whilst unflanged males actively pursue females to increase reproductive success but actively avoid rival flanged males[140]. Flanged males remain the most solitary, due to being highly intolerant of other males, as expressed through daily ‘long call’ vocalisation to reinforce spacing between neighbouring males[140], whilst sexually active females often avoid associations in order to avoid sexual coercion by males[106]. Overall, results presented illustrate the similarities in social behaviours of reintroduced and wild populations, demonstrating that rehabilitation has not detrimentally affected sociality.

Ecological factors can also influence sociality, as Sumatran forests are often more productive than comparative Bornean forests due to fertile volcanic soils and younger forests[145] thus creating a higher quality habitat and higher population density, often positively correlated with party size. Large party sizes of wild orangutans have also frequently been observed amongst strangling fig trees[106,48], as fig tree density positively correlates with increased soil pH, and in turn forest productivity, however this trend is not consistent across all populations[146]. Ultimately, sociality reflects the balance of social and ecological costs and benefits, whereby party sizes fluctuates opportunistically depending on the current pressures faced.

Rehabilitation does however influence dietary composition, particularly concerning a relatively low levels of fruit consumption, when compared to fully wild counterparts. Low fruit consumption levels are likely due to lack of wild fruits provisioned during rehabilitation, or lack of opportunities to consume hard to open or difficult to find fruits, specific skills which wild individuals would have gained from their mother. Due to the slow life history of Orangutans, offspring rely heavily on their mother for food during immaturity[57]. Infants solicit food from their mothers, which provides informational as well as nutritional benefits, further creating a form of parental investment[147]. Familiarisation with their mother's diet and foraging techniques promotes learning and allows offspring to develop foraging skills[148], as demonstrated by a decrease in food solicitation with ecological competence[147]. Skill acquisition via social and individual learning allows wild orangutans to possess the majority of the necessary feeding skills before they are completely weaned at the age of 5-7.5 years old[53,57]. Conversely, as most rehabilitant orangutans are orphaned during the early stages of infancy, around 2 years old, they lack vital mother-offspring learning experiences, and instead are taught by human-care givers during rehabilitation.

Across time of the year, and across time post-release, fruit consumption varied substantially. Most notably, the low fruit consumption of individuals in Batikap in 2015 is likely a response to the El Niño Southern Oscillation (ENSO) cycle, which is usually followed by a peak in fruit consumption, as a mast fruiting event typically follows prolonged drought[149]. However, analyses of phenology are necessary to validate this hypothesis, and to determine whether reintroductions during wild food abundance are more successful than during times of food scarcity. For example, individuals released during food scarcity may have increased difficulties finding familiar foods, adding to

the stress faced during reintroduction into an unfamiliar environment, and may therefore be less likely to survive. Furthermore, low fruit consumption has been a consistent trend amongst rehabilitant orangutans, possibly because the high nutritional value of cultivated fruits provided during rehabilitation allowed individuals to meet their metabolic needs with relatively low fruit consumption rates[150]. Thus, a continuation of this foraging strategy post-release, may result in either inadequate nutrition and subsequent reintroduction failure, or sourcing nutrients from alternative sources. Despite spending a similar amount of time feeding, fruit consumption was lower in TNBBBR and Batikap when compared to wild populations. Low fruit consumption in TNBBBR may be partly due to low fruit availability (Simon Husson, pers. comm.), however, low fruit consumption and subsequent high reliance on fall-back foods are consistent trends shown in both TNBBBR and Batikap as well as in Meratus and Sungai Wain[151]. Therefore, fall-back foods, such as meristematic tissue and leaves, potentially provide a key alternative source of nutrition, though future studies on the nutritional value of key fall-back foods are necessary to further verify this hypothesis. Consequently, more wild fruits should be introduced to individuals throughout forest school, in order to facilitate wild food recognition and to create more natural diets.

Overall, evidence suggests that reintroduced orangutans display behavioural flexibility as they rapidly settle into patterns of behaviour similar to that of fully wild individuals. This demonstrates that despite early life history, and a substantial amount of time spent in human-facilitated rehabilitation, orangutans are capable of fully independent survival once reintroduced into the wild. However, aberrant foraging behaviour, particularly less time spent feeding and lower fruit consumption, illustrates that improvements to rehabilitation are necessary to further improve post-release success. Therefore, the addition of more wild fruits provisioned during rehabilitation, will aid foraging skill acquisition, and increased post-release monitoring of individuals who did not attend forest school are key recommendations for improving reintroduction effectivity, ultimately reinforcing the value of reintroduction as a tool for orangutan conservation.

Chapter 3: Dispersal and ranging behaviour of reintroduced orangutans in Central Kalimantan, Indonesia.

3.1. ABSTRACT

The spatial distribution of a population, shaped by individuals' movements provides vital information on habitat quality, distribution of resources, and sociality. In reintroduction-based conservation programmes, understanding the movements of individuals following reintroduction is vital in determining the potential for re-establishing viable populations. Investigating the dispersal behaviour of semi-solitary, reintroduced orangutans into Bukit Baka Bukit Raya National Park, and Bukit Batikap Conservation Forest, Central Kalimantan, Indonesia, provided evidence for distinct dispersal strategies, leading to the identification of residents, commuters and wanderers. My results provide evidence for flanged male dispersal, and female site fidelity, similar to the behaviour seen among wild populations. However, kernel density estimates of individuals' annual home ranges were often larger than those for fully wild orangutans in comparable habitats. This study provides information on the space use of the release site, vital for assessing over-crowding risks, and identifying future reintroduction locations. Ultimately, understanding post-release behaviour and the subsequent demographic distribution is critical for improving the effectivity of future reintroduction protocols.

3.2. INTRODUCTION

The movement of an animal within a given area can provide information on social dynamics and the spatial and temporal distribution of essential resources. Analysing the movement of an individual in response to changes in resource availability or in human-modified landscapes is vital for aiding conservation strategies. In particular, information on movement is useful for identifying key habitats, areas of potential resource depletion or factors causing fragmentation, for example analyses of the movement of female loggerhead sea turtles (*Caretta caretta*) identified key areas of space-use outside of the protected area[152]. As a result, extensions to the protected area and stronger regulations to the marine area were recommended to ensure the protection of the species. Additionally, analyses of the movement of bumblebees

identified that roads restrict movement, and subsequently fragment potential foraging areas[153]. Therefore, a landscape-level management approach covering heterogenous habitats is necessary for the conservation of species relying on spatially or temporally dynamic resources.

Understanding animal movement is particularly vital for reintroduction strategies by understanding how individuals respond to a novel environment and gather information. Analysing space use and dispersal in response to reintroduction, or in human-modified environments aids the understanding of the spatial requirements of a population, vital for conservation management and assessing habitat suitability. The reintroduction of multiple individuals into a given location creates an artificial demographic distribution, therefore it is critical to determine whether patterns resemble those typically seen among wild populations. Understanding whether individuals disperse, or remain surrounding the release location is critical for assessing overcrowding risks and subsequent resource competition. Ultimately, a longitudinal analysis of movement is necessary to develop an understanding of the immediate and long term impacts of rehabilitation.

Using Bornean orangutans (*Pongo pygmaeus*) as the study subject, I investigated how rehabilitation and reintroduction influenced post-release movement. A substantial number of orangutans are under immediate threat from deforestation, or are subjects of the pet trade, therefore rescue and rehabilitation are vital conservation tools for protecting this critically endangered species. Individuals rescued are primarily orphans, therefore lack the critical experiences and survival skills they would have otherwise learned from their mother, so must progress through human-facilitated 'forest schools' to develop ecological competence[11]. Upon the completion of forest schools, individuals are transferred to semi-wild pre-release islands, where they are free to roam and display independent survival skills, such as foraging and nest-building, but still have access to supplementary food. Then, reintroduction is used to re-establish viable populations in protected habitats, in order to reduce the threat of extinction.

The influence of rehabilitation on post-release ranging behaviour remains largely unknown, primarily due to the lack of post-release monitoring. Previous orangutan reintroduction attempts using the 'soft-release' strategy (continuation of food

provisions) have failed due to a reduced foraging effort and ranging behaviour focussed towards feeding platforms[86]. Furthermore, unregulated tourism at reintroduction sites has also led to behavioural abnormalities and social stress from overcrowding at feeding platforms[81]. Therefore, investigating reintroduction attempts following the hard release strategy (without food provisions) and a no tourism policy provides crucial opportunities to understand how reintroduced orangutans respond to a novel environment, without human interference. Ultimately, addressing the factors responsible for previous reintroduction failures, and investigating the subsequent outcomes will aid the improvement of reintroduction protocols.

In order to understand the spatial use of an environment over time, the term 'home range' is commonly used to define the area occupied by an individual. Home range studies often focus on quantifying home range size which depends on both the definitions of home range and the methods used to calculate them. Instead, research should focus on how to define a home range and how it is constructed through behaviour, before measurements of size and overlaps become meaningful[154]. The home range of an animal is often influenced by the spatial and temporal distribution and abundance of resources[155], but can also be affected by body size[156], sex[157], social activities[158] and landscape[159]. Home range is therefore an interaction between the environment and the individual's perception of that environment, influenced by experience. For reintroduced individuals, the additional factors of rehabilitation and reintroduction can also be responsible for influencing movement. Developing an understanding of the intrinsic and extrinsic factors effecting movement is necessary to create a robust understanding of space-use[160].

Many definitions of home range are based on the stability of an animal's spatial and temporal movement, creating a demarcated area[161]. For example, Seton (1909)[162] stated that "*No wild animal roams at random over the country: each has a home region even if it has not an actual home*", however, this does not account for an exploratory period prior to home range establishment. Burt (1943)[138] followed by stating "*it is only after they establish themselves, normally for the remainder of their lives, unless disturbed, that one can rightfully speak of the home range*", therefore two distinct periods of movement are identified, the exploratory period during dispersal, and settlement, creating a home range.

Exploration is a key process during dispersal from a natal home range, allowing an individual to gain information on the environment, characterised by no clear pattern of spatial use[139]. In most mammals, females exhibit natal philopatry, residing near the area they were born, which is ecologically and socially advantageous as it allows individuals to persist in familiar habitats and develop social bonds with neighbours (often relatives), without imposing costs of dispersal, and risking less suitable conditions[108,163]. Males on the other-hand, tend to disperse to reduce competition for resources and avoid inbreeding[164]. In particular, wild female orangutans display natal philopatry, creating clusters of related females with overlapping home ranges[109,165,166], whilst males derive reproductive benefits from dispersing away from relatives[106,167]. Mating behaviour is therefore a major determinant of dispersal and social organisation. Conversely, for reintroduced orangutans the key factor driving dispersal is reintroduction, whereby artificially created demographic distributions are created between non-relatives upon release, meaning a natural distribution does not occur. The dispersal behaviour of reintroduced orangutans during a critical adaptation period following release therefore offers insights into space-use and exploration of the forest prior to home range establishment.

Settlement is the process following exploration which creates a home range, whereby an individual constrains its movement to within a chosen area. The most widely accepted definition of home range was created by Burt (1943)[138] who defined it as "*that area traversed by the individual in its normal activities of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range*." However, for semi-solitary orangutans, occasional exploratory sallies to seek mates are necessary to increase reproductive fitness, and can therefore be considered part of their normal activities.

Due to variation in home range definitions, and disproportionate use of areas within the home range, core areas most utilized are also identified as they often contain abundant resources and are of greater significance to the animal[168]. The subsequent movement of individuals post-release can then indicate the adherence to natural social organisations, or reveal behavioural differences between reintroduced and wild populations, vital for assessing reintroduction success. Moreover, overlaps between

neighboring individuals of a semi-solitary species suggests social tolerance and identifies key areas of the environment, necessary for understanding resource use.

This study aims to investigate whether reintroduced orangutans display release site fidelity, disperse far from their release point, or wander nomadically without a fixed range, aiding the understanding of space use during the critical exploratory period following release. I predicted that reintroduced individuals, particularly females will display site fidelity to their release point, similar to wild females often remaining adjacent to their mothers range[56]. Then, identifying behavioural patterns consistent with home range establishment will reveal the factors facilitating, or inhibiting settlement. I predicted that reintroduced orangutans will undergo a period of exploration in order to familiarise themselves with their surroundings prior to home range establishment. Estimates of home range size depends greatly on the method used, therefore I used different computational methods to help develop robust models of home range behaviour specific to reintroduced orangutans, comparable across sites. For example, grid squares are often used to calculate home range size and utilisation, which involves superimposing a grid over a research area and totalling the squares in which an individual was recorded in[169–171]. However, the size of the grid squares influences range size estimates, as large grids tend to over-estimate size. Additionally, calculations do not include any grid squares which individuals were not recorded in, but inevitably travelled through. Other methods include creating a circle using the two locations with the greatest distance between them as the diameter, however, home range estimates are likely to be over-estimated as ranges are unlikely to be precisely circular[170,172]. Studies using various methods to calculate range sizes have revealed that using polygons is a more conservative and biologically meaningful estimate due to representing the shape of the range and increasing in accuracy with increasing sample sizes[170]. Further, using kernel density estimates to reveal the utilisation distribution is favoured as it is likely that an animal does not use all areas of its range equally, though estimates are influenced by sample size and bandwidth selection[173,174].

Further, calculating the degree of overlap between conspecifics will identify potential over-crowding risks, as well as help develop an understanding of key areas within the environment. Ultimately, comparing the range behaviour of reintroduced orangutans to wild orangutans in comparable habitats will reveal the extent to which human-

facilitated rehabilitation influences post-release behaviour, contributing to assessments of reintroduction success. Results obtained will then help to produce recommendations for improving future reintroductions and post-release monitoring.

3.3. METHODS

3.3.1. Study site and subjects

This study took place at the Borneo Orangutan Survival (BOS) Foundation's Central Kalimantan reintroduction sites Bukit Baka Bukit Raya National Park (TNBBBR) (0°52'S, 112°30'E) and Bukit Batikap Conservation Forest (Batikap) (0°2'N, 113°31'E). I aided data collection, alongside a team of post-release monitoring assistants in TNBBBR. Data from previous reintroductions at Batikap were also analysed, then compared to raw data from wild populations in Sabangau National Park, Central Kalimantan (2°19′S, 113°54′E), and Gunung Palung National Park, West Kalimantan (1°13'S, 110°7'E). Both reintroduction sites are homogenous lowland mixed dipterocarp forests, whilst Sabangau is a homogenous peat swamp forest. Gunung Palung is a heterogenous forest, though primarily consists of a mixed dipterocarp forest. The study subjects in TNBBBR and Batikap have all undertaken stages of rehabilitation, though age at rescue influences the time spent in rehabilitation (See Appendix A and B). All subjects from Sabangau and Gunung Palung are fully wild individuals, primarily residents of the study area.

3.3.2. Data collection

All reintroduced orangutans are fitted with a small, Very High Frequency (VHF) radio transmitter implanted subcutaneously on the dorsal neck region[115], as external collars are tags have proved to be unsuitable for the morphology and behaviour of orangutans[175]. The device, created by the Research Institute of Wildlife Ecology in Vienna (FIWI), takes approximately 25 minutes to be surgically implanted, therefore can be performed during pre-release veterinary health checks, and poses no adverse effects to the behaviour or health of the individual[84]. The transmitter is on a low-power-

timer-circuit which becomes active at 8am until 4pm, to allow for a battery life of three to five years. The unique ID of each individual can be detected from 600m away on flat terrain or 1.5km from hilltops and open areas[175] by a BioTrack SIKA radio tracking receiver unit.

Small groups of approximately six individuals are released at 3 month intervals, at predetermined locations along river banks, spaced 1-2km apart. The reintroduction study areas are dissected into a grid system of transects at approximately 200m intervals, which allows the post-release monitoring team to check signals of all individuals at each interval throughout the forest. Once a signal is received, the focal individual is located by following the direction of the signal, aided by visual searching and then followed until a night-nest is made. GPS coordinates of the location of the focal are recorded at 30-minute intervals, creating a daily travel path, meaning coordinates are repeated if the focal has remained stationary. Methods conform to the BOS post-release monitoring Standard Operating Procedures, which are based on the Sabangau orangutan behaviour Standard Operating Procedures 2016. Due to the reclusive, arboreal nature of orangutans, finding individuals in difficult terrain can be challenging, meaning individuals are often not followed consistently each month, instead data must be taken opportunistically. Consequently, limitations in data analysis exist whereby the location of an individual between follows is unknown, and therefore estimated based on previous locations, creating a level of uncertainty.

3.3.3. Data analysis

3.3.3.1. Age sex classification

To investigate differences in movement patterns between sexes and developmental stages, four Age-sex classifications were used. Sexually active females (SAF) are defined as sexually mature, parous adults, either accompanied by an infant or without offspring as a result of juvenile independence, or early death of the infant. Non-sexually active females (NSF) are defined as sexually maturing or mature, nulliparous females, travelling independently. Flanged males (FM) are defined as morphologically

distinct, mature males, displaying fully developed cheek-pads (flanges), laryngeal throat sacs and larger body size. Unflanged males (UFM) are defined as sexually maturing or mature males undergoing developmental arrest, therefore do not display flanged traits, though early signs of cheek-pad development may be visible.

3.3.3.2. Dispersal from release point

Handheld GPS receivers often display a degree of spatial inaccuracy, whereby the discrepancy between the true coordinates and those recorded by GPS is affected by canopy cover, tree density and terrain[176]. I therefore identified outlying points, usually out of the study area, using ArcMap 10.5.1[177], and confirmed them by comparison to prior and subsequent positions and corresponding behavioural data, then subsequently removed them to reduce spatial inaccuracy. Uncertainty in location accuracy still remains, though studies have reported that 99% of errors in high-canopy areas are less than 7.98 meters[176], which is relatively small in regards to orangutan spatial movements.

To analyse exploratory movement, I defined dispersal as movement away from the release point, therefore the dispersal distance between the release point and each subsequent location was plotted against time post-release[178]. Fluctuations in the dispersal plots correspond to varying distance travelled relative to the release point. A horizontal line can either depict a stationary individual, or travel equidistant to the release point, therefore trajectory maps were used to confirm movement. I then categorised individuals in regards to the three most common wild orangutan spatio-temporal movement patterns; *Residents*, *Commuters* or *Wanderers*, adapted from Rijksen and Meijaard (1999)[37]. For wild orangutans, the literature defines *residents* as those who are found in one particular area for most of the year, over many years, whereas *commuters* are seen regularly for several weeks or months each year, over many years and appear to live nomadically. *Wanderers* are those seen very infrequently, or just once, over a period longer than three years, and many never return to the area[37]. I modified the definitions of the wild orangutan movement pattern categories to apply to reintroduced orangutans who are released in groups at pre-determined locations, therefore do not have a natal range. I used categorisation to determine whether individuals display site philopatry and become *residents*, roam

without establishing a fixed range, similar to *commuters*, or disperse far from their release point. I therefore defined *residents* as individuals remaining less than 1km from their release site for most of the year, though brief excursions once or twice are expected. I used a period of 12 months post-release to account for variation in resource availability over annual seasonality, and a 1km radius from the point of release to encompass a 314 hectare area, representing the approximate size of the home range of a wild female Bornean orangutan of the same sub-species (*Pongo pygmaeus wurmbii*), in a homogenous habitat[56]. Consequently, movement consistently within a 1km radius of the release point implies *residents* are those who have established their range surrounding their release point. I defined *commuters* as those whose dispersal distance consistently fluctuates over a 2km threshold throughout the year, and appear to live a nomadic existence. For example, individuals may have an established core range, but often travel and return to their release point as part of their wider range or brief excursions. 1km and 2km cut-off points serve as a basis for distinguishing dispersal strategies, but do not restrict range size in each category. I then defined *wanderers* as those displaying one-way dispersal from their release point, often out of the study area during the immediate months following release, and have not been recorded to have returned closer to the release point. As a paucity of data, an individual could generate inaccurate classifications, therefore I only used individuals with consistent data over 12 months post-release to categorise dispersal patterns (with the exception of *wanderers* who often disappeared within the first few months and did not return).

3.3.3.3. Home range establishment

The point at which an orangutan's home range becomes established is difficult to determine owing to no distinct barrier restricting movement, and no territoriality. Plotting all known locations of an individual provides a sample of space-use, used to estimate overall ranging behaviour. Frequent returns to a highly utilised area indicate a preference for a core area, thus the stability of a single core range over time provides evidence for home range establishment, differentiated from multiple centres of activity implying exploratory behaviour.

The size of an individual's estimated home range is influenced by the number of GPS points, the length of study and size of the study area[170,174,179], as well as forest type, heterogeneity and sub-species[56], therefore I restricted home range analyses to individuals with a minimum of 20 follows per year, and annual home range size was implemented to account for the differences in study length between sites. Data across the first year post-release consisted of 10 individuals from Batikap and 8 individuals from TNBBBR. Using the same data analysis techniques, raw data from wild populations of the same sub-species (*P. p. wurmbii*) were used as a comparison of range size. 33 annual home range estimates were calculated from six male and six female wild orangutans in a homogenous peat swamp forest in Sabangau National Park, Central Kalimantan (2°19′S, 113°54′E), used to compare range size in homogenous forests. 13 annual home range estimates were calculated from five female individuals in a heterogenous primarily mixed dipterocarp forest in Gunung Palung National Park, West Kalimantan (1°13'S, 110°7'E) used to compare range size in dipterocarp forests.

GPS locations were plotted and projected to Universal Transverse Mercator (UTM) zone 49s using the 'rgdal' package in R[180]. Total range size was calculated using Minimum Convex Polygons (MCPs) at 100% volume contours, which create a polygon by connecting the outermost points of each individual. MCPs assume uniform spatial use throughout the range and are sensitive to excursions and the overall shape of the range, but it is a widely used method allowing explicit comparisons between sites, therefore prove valuable when used alongside other methods[181]. Fixed Kernel Density Estimates (KDEs)[173] at 95% and 50% volume contours were also created using the 'adehabitatHR' package[182], which estimate a utilisation distribution based on the distribution of observed locations and size of the smoothing parameter (h). Volume contours set at 95% and 50%, though arbitrary, exclude excursions, encompass core areas most utilized respectively, and are consistent with published data, thus improving comparisons[183]. Least-squares cross validation (h_{LSCV}), and the default reference bandwidth (h_{ref}) methods were first used to determine the smoothing parameter of the utilisation distributions[173]. I then set a fixed smoothing parameter value of h=250 calculated ad-hoc by averaging the minimum smoothing parameter needed to create an unfragmented 95% volume contour utilisation distribution for each individual, to allow comparisons between individuals. To compare annual home and

core range sizes across sites, I used a one-way ANOVA to determine the effects of site, followed by Tukey post-hoc tests with Bonferroni correction to determine differences between each site. Overlaps were investigated by calculating the area shared by each dyad combination of individuals used in analyses, then imported into ArcGIS ArcMap 10.5.1[177] and plotted onto maps of the study sites.

3.4. RESULTS

3.4.1. Dispersal strategies

Quantification of the post-release movement patterns provides evidence for distinct dispersal strategies. Individuals classified as *residents* displayed site philopatry, whereas *wanderers* dispersed far from the release point and *commuters* displayed an intermediate strategy of occasionally returning to their release point (Figure 3.1).

From the 130 individuals in Batikap that had been reintroduced 12 months prior to the time of study, 31 had consistent GPS data across the first 12 months post-release. From these individuals with sufficient data, 14 were classified as *residents* (SAF= 8, NSF=5, UFM=1; Figure 3.1a), six were *commuters* (NSF=2, FM=2, SAF=1, UFM=1; Figure 3.1b), nine were *wanderers* (SAF=4, NSF=2, UFM=2, FM=1; Figure 3.1c), and two individuals did not display large fluctuations in dispersal distance, but were consistently found approximately 3km away from release site, therefore were separately identified as '*neighbours'* (NSF=1, UFM=1). Only the first three release groups from TNBBBR, totalling 26 individuals, had data spanning over 12 months post-release, and only 16 had sufficient data to allow categorisation, resulting in seven individuals categorised as *residents* (NSF=3, UFM=3, SAF=1; Figure 3.1a), five as *commuters* (NSF=4, SAF=1; Figure 3.1b) and four as *wanderers* (FM=4, UFM=1; Figure 3.1c). It is important to note that these categories were only possible for the subset of individuals which there were sufficient data. Given that they were not regularly found within the study area, the majority of uncategorised individuals are likely to be *wanderers* that have dispersed out of the study area, or *commuters* who return infrequently.

Across both sites, the majority of *residents* (17/21) were female, providing evidence for female release site philopatry. *Commuters* also often utilised the area surrounding

the release site therefore display some degree of site fidelity, but ranged over a larger area. Conversely no flanged males were categorised as *residents*, but four out of the five flanged males in TNBBBR and one out of three in Batikap were *wanderers*, and only two were *commuters*, meaning remaining individuals with insufficient data are likely to have also dispersed from the study site.

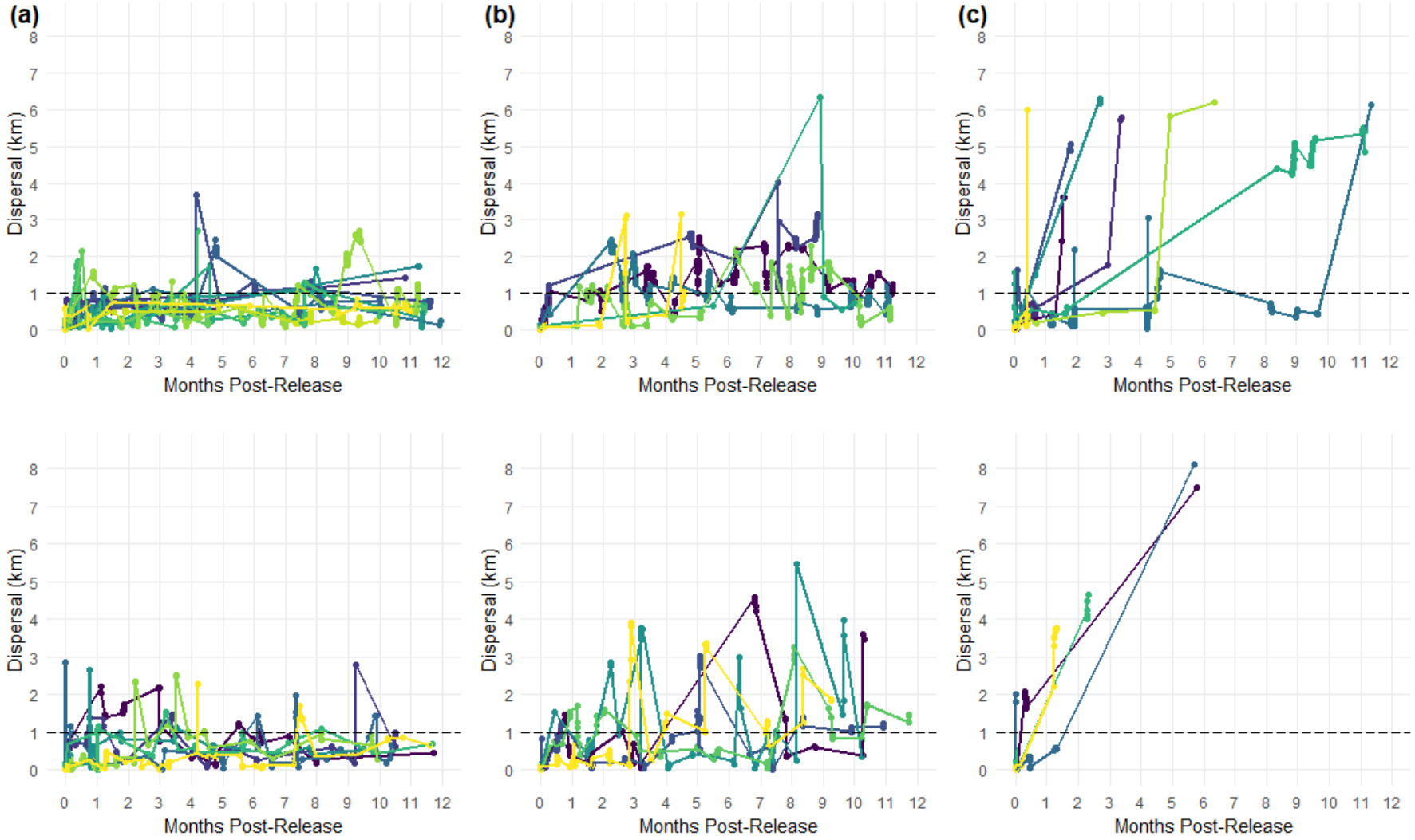

Figure 3.1. Dispersal (km) from release point across 12 months post-release, for individuals in Batikap (above) and TNBBBR (below) categorised as (a) Residents, (b) Commuters, or (c) Wanderers. Dashed horizontal line represents 1km guide used for categorisation. Line colours represent different individuals

3.4.2. Home range

3.4.2.1. Home range establishment

Home range establishment is a gradual process whereby exploratory movement declines over time, making it difficult to isolate distinct time points at which home ranges are established. Nevertheless, the maintenance of a consistent distance from release site provides a useful indication of movement stability within a chosen area. Residents therefore display home range stability and settlement from the time of release, characterised by consistent movement within a 1km radius of the release point, with only occasional temporary excursions (Figure 3.2a). Maps of movement trajectories reinforce this concept by illustrating a single core area most utilised surrounding the release point (Figure 3.2b). Conversely, commuters often have multiple centres of activity with no single defined core range, thus implying either a continuation of exploratory behaviour, and no established home range (Figure 3.3), or a single centre of activity with many excursions, implying a large home range. The two individuals identified as neighbours display initial exploratory behaviour, followed by a consistent dispersal distance and single defined core, similar to that of residents (Figure 3.4), exemplified by Ebol, who locates a suitable area after two months post-release then remains within this area, signifying home range establishment. The home range establishment of wanderers remains unknown due to lack of data. Overall, home range establishment of reintroduced orangutans can be characterised by a consistent distance from release site, with a single core centre of activity.

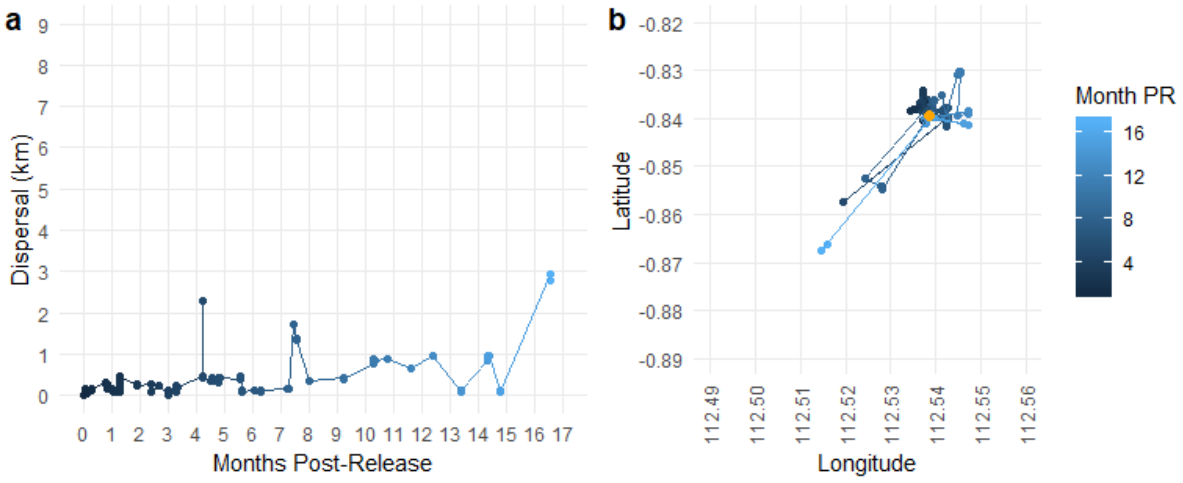

Figure 3.2. The (a) dispersal distance and (b) movement trajectory of 'resident' Winda across 17 months post-release (PR). Orange point illustrates release location.

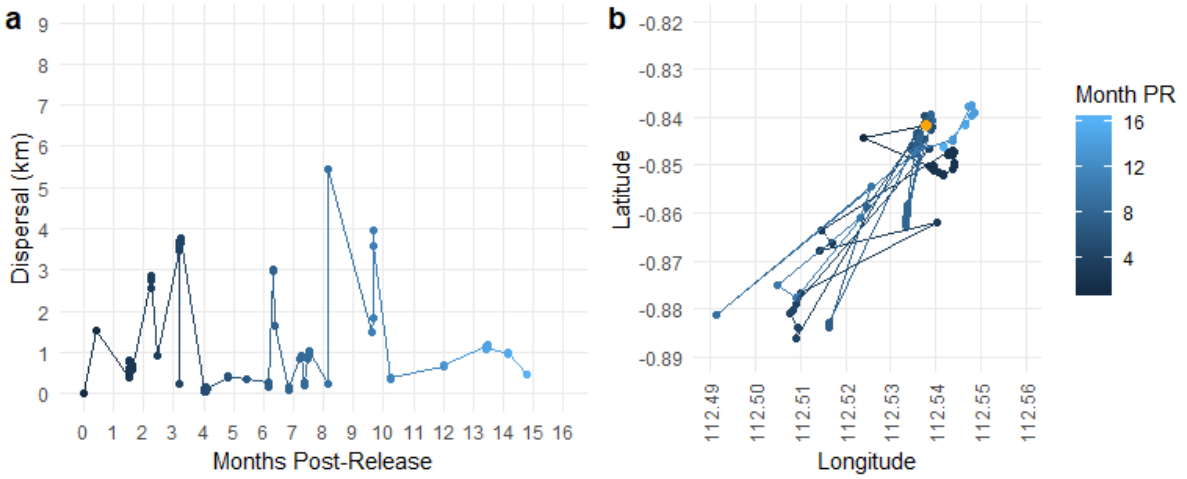

Figure 3.3. The (a) dispersal distance and (b) movement trajectory of 'commuter' Ewa across 16 months post-release (PR). Orange point illustrates release location.

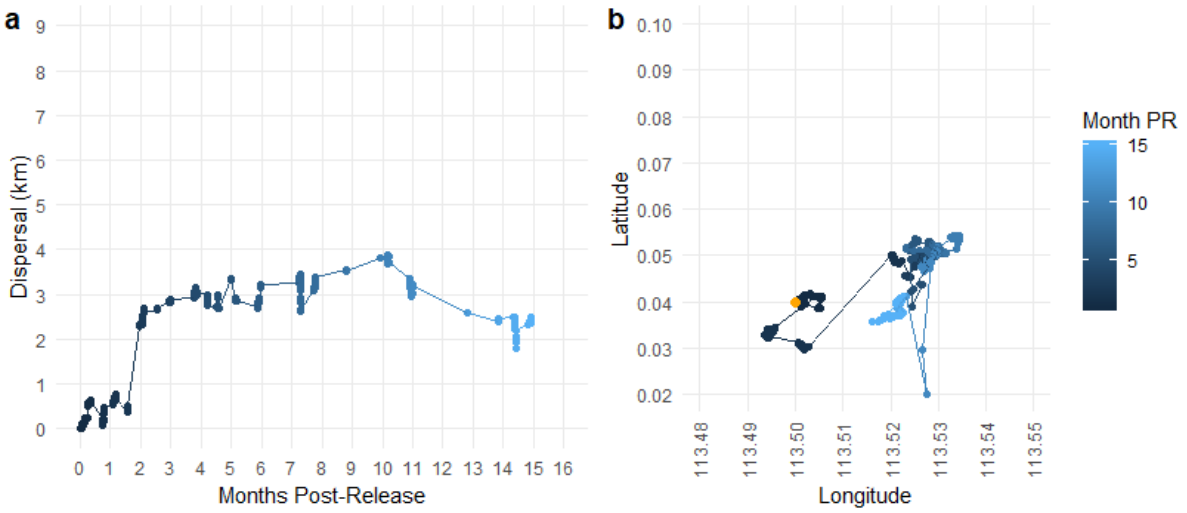

Figure 3.4. The (a) dispersal distance and (b) movement trajectory of 'neighbour' Ebol across 15 months post-release (PR). Orange point illustrates release location.

3.4.2.2. Range size

Estimates of home range size can vary substantially depending on the computational methods used. Kernel Density Estimates with the h_{LSCV} method considerably under-smoothed points as it produced severely fragmented home ranges, with small areas. The h_{ref} method produced more meaningful home ranges, due to creating unfragmented areas, but bandwidth varied between individuals preventing inter-individual comparisons. The h_{250} method therefore provided a meaningful estimate

similar to the h_{ref} method, but the consistent bandwidth allowed comparisons between individuals and across sites (Table 3.1).

Table 3.1. The mean Kernel Density Estimates (hectares) at 95% (Home range) and 50% (Core range) volume contours, for females (F) and males (M) at each site (n=number of annual range estimates), with smoothing parameters calculated by the reference bandwidth (h_{ref}), Least-Squares Cross Validation (h_{LSCV}) and ad-hoc value of 250 (h_{250}). (± Standard Error)

		h_{ref}		**h_{LSCV}**		**h_{250}**		**MCP**
		95%	50%	95%	50%	95%	50%	100%
TNBBBR	*F*	**1257**	**228**	**107**	**17**	**729**	**130**	**883**
	(n=8)	(±207)	(±41)	(±24)	(±5)	(±76)	(±19)	(±108)
	M	**840**	**159**	**48**	**7**	**562**	**113**	**684**
	(n=2)	(±172)	(±7)	(±3)	(±1)	(±14)	(±32)	(±335)
Batikap	*F*	**465**	**99**	**68**	**9**	**501**	**106**	**528**
	(n=9)	(±70)	(±19)	(±13)	(±2)	(±48)	(±15)	(±54)
	M	**687**	**141**	**86**	**12**	**534**	**112**	**644**
	(n=3)	(±212)	(±34)	(±21)	(±4)	(±64)	(±12)	(±95)
Gunung Palung	*F*	**285**	**69**	**66**	**10**	**397**	**96**	**271**
	(n=13)	(±95)	(±36)	(±29)	(±5)	(±84)	(±36)	(±109)
	M	-	-	-	-	-	-	-
		-	-	-	-	-	-	-
Sabangau	*F*	**200**	**54**	**97**	**25**	**316**	**79**	**192**
	(n=26)	(±28)	(±7)	(±15)	(±4)	(±25)	(±7)	(±35)
	M	**442**	**106**	**151**	**35**	**505**	**120**	**385**
	(n=7)	(±62)	(±14)	(±27)	(±8)	(±55)	(±12)	(±79)

Estimates of range size for TNBBBR and Batikap were calculated using all residents and only the commuters when they displayed home range establishment behaviour, such as a single core area of activity, and relatively small fluctuations in dispersal distance. Using the h_{250} method, comparisons to wild populations of the same sub-species (*P. p. wurmbii*) in the homogenous peat swamp forest of Sabangau, and in the heterogenous mixed dipterocarp forest of Gunung Palung revealed a significant difference among annual home range size between sites (One-way ANOVA; F_6= 15.31, $p<0.001$). Tukey post-hoc tests revealed significant differences between the females in TNBBBR and the females in each of the other sites, as well as differences between TNBBBR females and Sabangau males (Figure 3.5). In contrast, only the core range sizes, of females in TNBBBR and Sabangau significantly differed (One-

way ANOVA; F_6= 3.45, p=0.005). Overall, the annual home range sizes of reintroduced orangutans across the first year post-release were larger than those of wild orangutans in a homogenous forest (Sabangau), and of those in a predominantly dipterocarp forest (Gunung Palung).

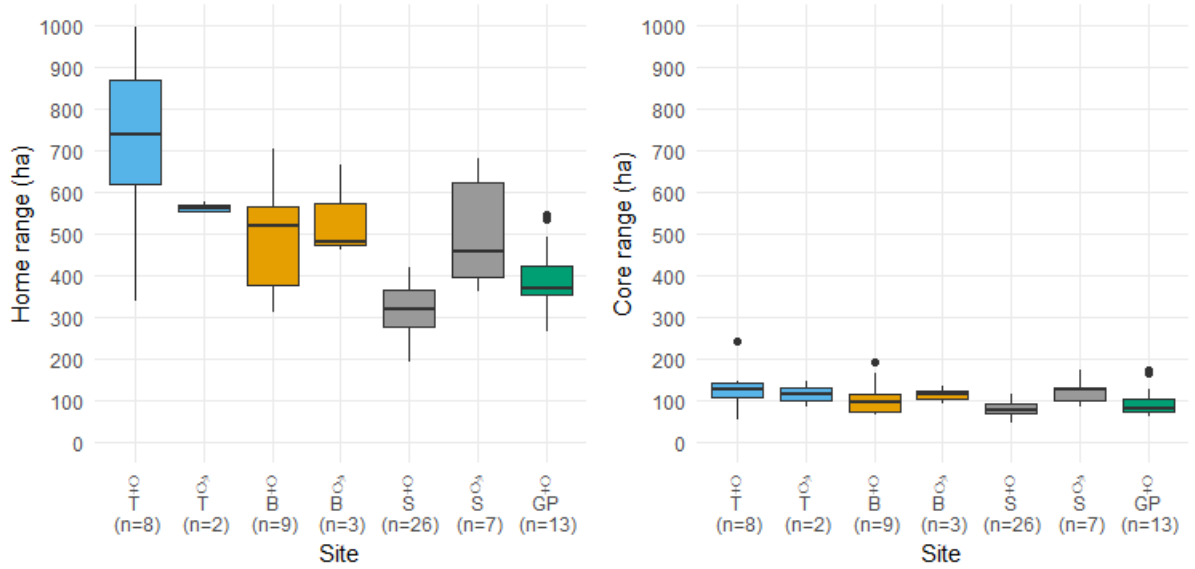

Figure 3.5. The area (hectares) of 95% (Home range) and 50% (Core range) volume contour Kernel Density Estimates (h=250) for males and females at reintroduction sites TNBBBR (T) and Batikap (B), and wild sites Gunung Palung (GP) and Sabangau (S). (n=number of annual range estimates)

3.4.2.3. Overlaps

Individuals in TNBBBR and Batikap primarily utilise areas surrounding the rivers, though this may partly be attributed to individuals becoming more difficult to locate and follow, with increased distance from the rivers. The proportion of home range overlap between pairs of neighbouring individuals varied substantially from 0-97%, (mean 28% ±1.89), whilst overlaps between core ranges was lower ranging from 0-95% (mean = 12% ±0.83). Most notably, the home range of Markisa and independent female offspring Manggo overlapped 97% providing evidence for the development of independence, and the 'petal hypothesis' whereby the ranges of related females highly overlap[166]. Multiple individuals with overlapping ranges means the total proportion of shared area is greater than the average dyad overlap, particularly within TNBBBR

(Figure 3.6). The actual number of overlapping ranges is greater than those depicted by Figure 3.6, as other individuals with insufficient data to estimate range also, at least partially, utilise these areas surrounding release points. Thus, a larger range size may be a response to resource competition from a high density of overlapping individuals remaining within these areas.

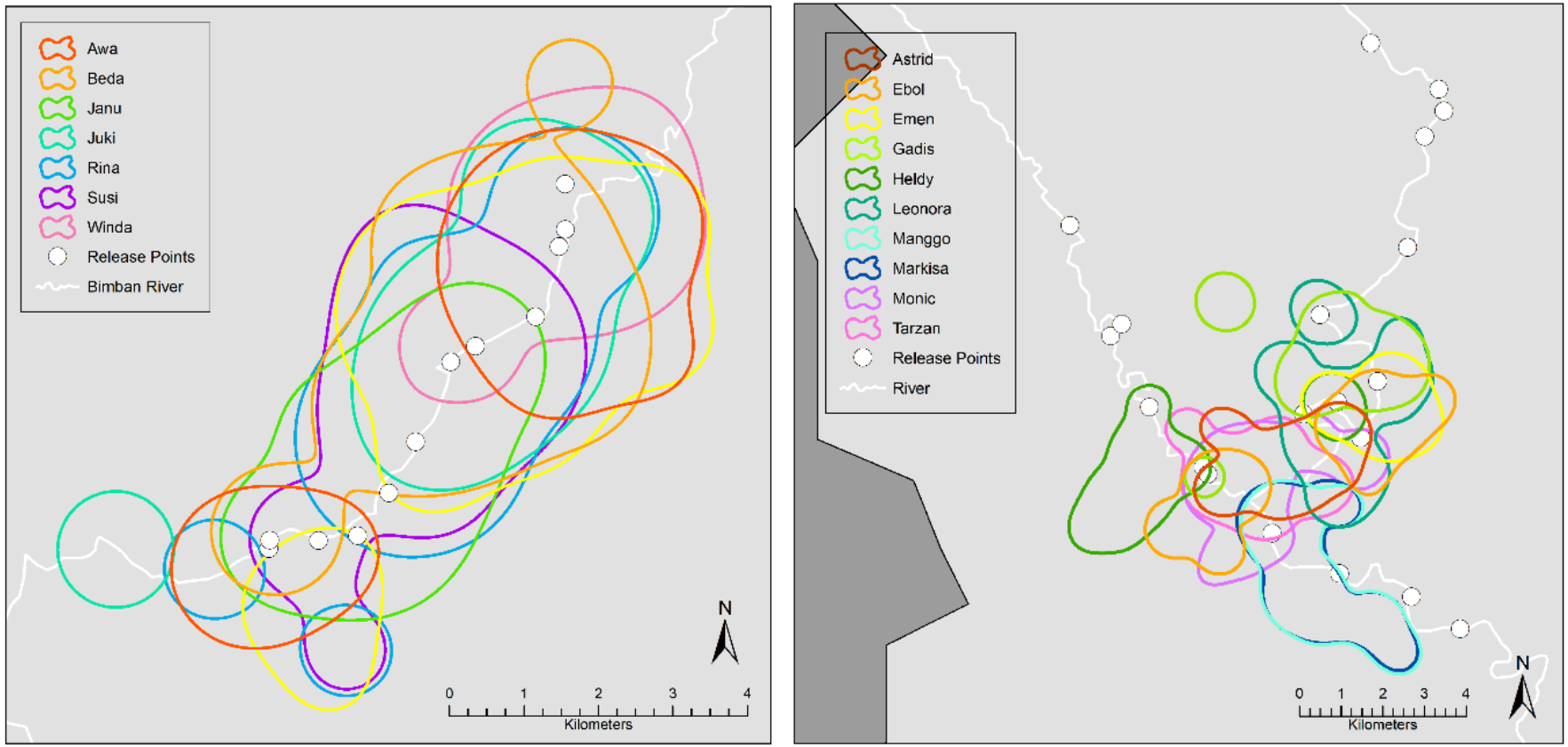

Figure 3.6. Map of 95% volume contour Kernel Density Estimates for eight individuals in TNBBBR (left) and ten individuals in Batikap (right).

3.5. DISCUSSION

Reintroduction is a key conservation tool used to reduce the threat of extinction by establishing new self-sustaining populations in protected areas. Understanding dispersal patterns, followed by home range establishment explores how reintroduction protocols influence the demographic distribution of the population. Overall, evidence was provided for the categorisation of distinct dispersal strategies; *residents, commuters*, and *wanderers*.

Residents occupied a defined are within a 1km radius of their release point, throughout a period of 12 months post-release, though occasional excursions are expected due to seasonal variation in food abundance. Overall, *residents* were mostly female, providing evidence for female release site philopatry, similar to natal philopatry seen in wild populations[108], despite lack of relatedness between individuals. Similarly, *neighbours* displayed behaviour consistent with definitions of wild orangutan *residents*, by occupying a distinct area throughout the year, however were found two to three kilometres from release point. This is likely to be a response to over crowding around release areas, in order to reduce resource competition. Overcrowding most likely occurred due to the release site philopatry displayed by residents, therefore may create risks of food depletion if more individuals were reintroduced within this area. Subsequently, it may be beneficial to release fewer individuals at each release point, and increase spacing between groups to minimise overcrowding.

Commuters also often utilized the area surrounding the release point, suggesting that they may also show philopatric tendencies, though to a lesser extent than residents. *Commuters* can therefore either have large ranges encompassing release site and beyond, or travel without an established range, including multiple centres of activity instead of a single core area[170], likely a response to temporal availability and spatial distribution of food sources, particularly within areas of with a higher density of individuals.

The categorisation of flanged male wanderers and lack of sightings of the remaining flanged males provides evidence for male dispersal, similar to that recorded in wild populations, whereby individuals disperse to reduce the likelihood of inbreeding, and to reduce male-male competition[109,165,184]. Notably, two flanged males from TNBBBR dispersed and entered a village 8km away from their release point, resulting in them

being translocated back to the rescue centre. The dispersal of these males created risks of human-wildlife conflicts, however previous socialisation visits to the village aided conflict resolution. As a consequence, the likelihood of flanged male dispersal should be incorporated into reintroduction strategies to minimise risks to all those involved. Conversely, the existence of female wanderers is rarely observed in wild orangutans, though for reintroduced orangutans, may be attributed to male harassment avoidance[185], or a response to overcrowding around the release points and subsequent food competition.

Individuals unaccounted for due to dispersal away from the study site is a consistent trend within orangutan reintroduction projects[86], meaning dispersal patterns, home range establishment, and mortality rates remains unknown, limiting the assessment of reintroduction success. However, from consistent use of the study sites for radio-tracking and data collection, I can tentatively conclude that individuals with insufficient data but confirmed survival are not residents, but instead may still exhibit exploratory behaviour and only occasionally return to the study site. In conclusion, lack of data limits our understanding of whether wanderer and commuter dispersal strategies are effective or detrimental to reintroduction success. Although, the confirmed survival of individuals within each classification provides evidence for the behavioural flexibility of orangutans, and promotes optimism regarding the effectivity of reintroduction.

Home range establishment of orangutans is a rarely studied concept, therefore the reintroduction of ex-captive orangutans into a novel environment provides numerous opportunities to develop an understanding of factors effecting home range selection. The point at which a home range becomes established is difficult to determine owing to no specific boundary, however, the reduction of exploratory movement and spatial stability of a single core area, calculated via dispersal distance, provides evidence for settlement. *Residents*, by definition, quickly establish their range around the release point, displaying minimal exploratory behaviour. *Commuters* on the other hand, take longer to establish a range due to prolonged exploratory behaviour, which may be a response to the high density of residents and resource competition.

The size of established home ranges of wild orangutans is often attributed to resource distribution, which is affected by forest type and heterogeneity, as well as taxonomic affiliation[56] and sex[186]. Those in heterogenous habitats often range over a larger area

to utilise fruiting patterns which vary between habitat mosaics and seasonality[56]. Sumatran orangutans *P.p.abelii* tend to have the largest ranges, followed by Bornean orangutans *P.p.wurmbii* and then *P.p.morio*. It is likely that a large proportion of rescued individuals originated from peat swamp forests in Central Kalimantan, therefore may have retained knowledge from early life experiences and may subsequently behave similar to their native population. Controlling for sub-species and forest type limited comparisons to Gunung Palung, a heterogenous habitat containing primarily mixed dipterocarp forest, as there is currently no data available for wild *P. p. wurmbii* in a homogenous mixed dipterocarp forest. Controlling for sub-species and habitat homogeneity, comparisons to Sabangau revealed that wild orangutans in a homogenous habitat have significantly smaller ranges than reintroduced individuals. Overall, despite controlling for sub-species, forest type and heterogeneity, the home ranges of reintroduced orangutans were consistently larger than comparable wild conspecifics, though core ranges were similar. The effects of reintroduction therefore explain the differences seen, whereby a high density of individuals with highly overlapping ranges remain around release sites, potentially increasing scramble competition for food resources. Similarly, large home ranges of wild orangutans have also been correlated with high density, due to the increase of competition for food[56], therefore wider movement covers a greater number of food sources, reducing the risk of resource depletion. Subsequently, high levels of overlap, particularly among females, provides evidence for social tolerance, despite relatively low levels of social interactions, however, an increased risk of resource competition may hinder reintroduction success.

Ultimately, human-facilitated rehabilitation and reintroduction has an influence on post-release behaviour, particularly on the range size and subsequent social distribution of a newly founded population. Reintroduced orangutans, particularly females, display release site philopatry, similar to natal philopatry recorded in wild populations, whilst flanged males are more likely to disperse far from the release location, similar to the dispersal of wild males to reduce inbreeding[109]. Therefore, despite substantial human influence throughout early life, reintroduced orangutans display dispersal patterns similar to that of wild conspecifics. Further, the hard-release strategy of no supplementary feeding ensures individuals exhibit independent foraging and exploratory behaviour, rather than remaining around feeding platforms, which

have proved to be detrimental to home ranging behaviour of individuals at other reintroduction sites[82,86]. However, reintroduced orangutans encompass larger areas than comparable wild populations, likely a response to a high population density. Overall this study identifies possible overcrowding risks if future individuals are released among areas of current high density, which highlights the importance of consistent post-release monitoring and assessment of reintroduction protocols, vital for improving future reintroductions.

Chapter 4: General conclusions and recommendations for future reintroductions

4.1. CONCLUSION

Orangutans (*Pongo spp*.) are classified by the IUCN as critically endangered with populations in decline. The conservation of remaining populations is therefore critical to reduce the threat of extinction. Though protection and preservation of rainforest habitats remains paramount, the number of individuals already affected by human induced factors such as deforestation and hunting, means rescue, rehabilitation and reintroduction is a critical tool for protecting individuals under immediate threat. Understanding the behaviour and ecological competence of reintroduced individuals is vital for assessing the influence of early life experiences, rehabilitation and reintroduction protocols. In this thesis I have revealed that longitudinal changes in behaviour occur, demonstrating that reintroduced individuals undergo an 'adaptation' period, whereby initial behaviour consists of increased sociality, reduced levels of feeding with elevated levels of resting and travelling. This behavioural difference was attributed to a combination of factors, namely rehabilitation protocols such as group living and provisioned food, and stress related to transport and reintroduction into a novel environment. However, the robust behavioural flexibility of the species was realised as individuals rapidly adjusted their activity budgets across the first three months-post release, resulting in behavioural stability resembling that of wild populations. Overall, the impact of rehabilitation and reintroduction only temporarily influenced post-release behaviour. However, differences in dietary composition compared to wild conspecifics remained, particularly, lower fruit consumption. Though dietary repertoire increased across time due to individuals consuming more different food items, the reliance on fall back foods such as meristem remained relatively high, suggesting individuals may not recognise or have the specific skills to forage for a sufficient number of wild fruits.

Furthermore, understanding the movement of individuals from their release point provided information on the spatial use of the forest, vital for understanding ecological and social requirements. The identification of residents with highly overlapping home ranges may be particularly useful for predicting over-crowding risks. A high density of

individuals following reintroduction, and subsequent food competition may have been responsible for the reduction in foraging rates. As individuals dispersed and density decreased, food intake also increased, suggesting high population density is a key factor constraining foraging behaviour. Improving the spatial distribution of release groups by reducing the number of individuals per group and increasing spacing between groups may be critical for aiding food intake during the adaptation period. The identification of wanderers, particularly flanged males was useful for predicting the chance of dispersal, vital for minimising potential human-wildlife conflicts. Overall, the illusive, solitary nature of orangutans limits consistent observations, restricting data collection. Though the introduction of radio telemetry lessens this limitation, improvements are needed to increase search radius. However, dispersal from the study area prevents data collection, and limits knowledge on the behaviour and outcome of those individuals.

Ultimately, this study provides new evidence of the immediate and long-term behaviour of reintroduced *P. p. wurmbii* in a homogenous mixed dipterocarp forest. Moreover, the factors identified influencing reintroduction success, such as adherence to IUCN guidelines, adequate skill acquisition, and sufficient post-release monitoring are applicable across species. This study also highlighted the effectivity of improved, well managed reintroduction protocols, further increasing the value of reintroduction as a tool for conservation.

Future studies should focus on locating individuals unaccounted for either by improvements to telemetry devices, or expeditions out of the study area in order to identify key factors influencing dispersal. Further, studies into the behaviour of individuals progressing though rehabilitation, particularly dietary composition and repertoire, as well as determining the nutritional value of fall-back foods would be essential for deciphering the factors influencing reduced fruit consumption.

4.2. RECOMMENDATIONS

Problem 1: *Reduced fruit consumption and high reliance on fall-back foods*.

Recommendations: Individuals rescued over the age of five generally do not attend forest school, therefore reduced success of this group is likely attributed to inadequate skill acquisition post-release, particularly foraging skills. Therefore, the introduction of specifically designed forest schools, in a semi-wild environment may serve as a beneficial alternative to socialisation cages, by using experienced individuals as demonstrators for wild food recognition and foraging techniques. Further, the addition of more wild fruits available throughout rehabilitation would be beneficial to aid recognition and improve foraging techniques. This would also reduce reliance on cultivated foods, minimise the chance of individuals taking food from villages or camp and aid the creation of a more natural diet.

Problem 2: *Over-crowding risks*.

Recommendations: The identification of distinct dispersal strategies is important for determining future release group candidates and release locations, as overcrowding can lead to competition, stress and resource depletion[86]. The identification of residents and the location of their core range should be calculated prior to subsequent releases to ensure sufficient distances between release points.

Problem 3: *Human-wildlife conflicts from dispersal out of study area*.

Recommendations: The likelihood of flanged males dispersing out of the release site and into neighbouring villages increases the risk of human-wildlife conflicts, therefore flanged males should be released out of range of other rival males, and far from villages. Overall the demographic distribution of the population should be calculated annually in order to identify where home ranges have been established, and where future reintroductions could occur.

Problem 4: Locating *individuals unaccounted for.*

Recommendations: Gradually increasing study site area, or conducting additional expeditions to remote locations, would aid the location of individuals unaccounted for. Additionally, the introduction of drones for nest surveys, and improvement of telemetry devices by increasing search radius, or use of Automated Radio-Telemetry Systems (ARTS)[187] are possible areas of improvement in order to locate dispersed individuals, vital for robust assessments of reintroduction success. The introduction of accelerometers[188] to detect changes in the velocity of the body over time would be beneficial for identifying stationary individuals (sick individuals or fatalities) as well as for improving analyses of changes in activity budgets, critical for investigating how individuals respond to reintroduction.

Problem 5: *Individuals residing around camp.*

Recommendations: A number of individuals located the research camps in TNBBBR and Batikap, and remained around the perimeter, often entering to steal food. In particular, a group of individuals were released close to camp in TNBBBR, therefore could hear the boats used to facilitate monitoring and could see human activity, hence travelled to investigate. Translocation was used to move two individuals in TNBBBR in order to reduce reliance on cultivated foods, and to eliminate human-wildlife conflict. However, ensuring groups are further than 1km from research camps would reduce the likelihood of this problem.

Problem 6: *Lack of phenology data.*

Recommendations: Phenology data analyses should be conducted as part of post-release monitoring, to ascertain whether reintroductions are more successful during times of food abundance rather than times of food scarcity. Furthermore, identifying key species of wild food sources will aid improving foraging skill training during rehabilitation.

APPENDICES

Appendix A: Profiles of individuals reintroduced into Bukit Batikap Conservation Forest.

Orangutan Name	Release Group	Release Date	Age-sex	Origin	Age at Rescue	Age at Release
Astrid	1	29/02/2012	SAF	Wild		14
Atsuko (Offspring of Astrid)	1	29/02/2012	UFM	Born in Batikap		0
Monic	1	29/02/2012	SAF	Semi-Wild		8
Messi (Offspring of Monic)	1	29/02/2012	UFM	Born in Batikap		0
Tantri	1	29/02/2012	NSF	Semi-Wild		9
Tarzan	1	29/02/2012	FM	Wild		25
Bang Jagur	1	31/03/2012	UFM	Wild		12
Bunga	1	31/03/2012	NSF	Semi-Wild		9
Heldy	1	31/03/2012	UFM	Semi-Wild		9
Ika	1	31/03/2012	NSF	Semi-Wild		10
Jojo	1	31/03/2012	UFM	Semi-Wild		8
Kali	1	31/03/2012	NSF	Semi-Wild		9
Komeng	1	31/03/2012	FM	Wild		22
Mama Tata	1	31/03/2012	SAF	Wild		22
Ompong	1	31/03/2012	FM	Wild		27
Tata	1	31/03/2012	UFM	Semi-Wild		9
Yaya	1	31/03/2012	NSF	Semi-Wild		9
Abam	2	09/08/2012	UFM	Semi-Wild		10
Jessica	2	09/08/2012	NSF	Wild		14
Mama Ebol	2	09/08/2012	SAF	Wild		21
Ebol (Offspring of Mama Ebol)	2	09/08/2012	NSF	Semi-Wild		8
Maradona	2	09/08/2012	FM	Wild		26
Onceng	2	09/08/2012	NSF	Wild		9
Sempung	2	09/08/2012	FM	Wild		22
Sumbing	2	09/08/2012	FM	Wild		23
Giant	3	01/11/2012	UFM	Semi-Wild		10
Gundul	3	01/11/2012	NSF	Semi-Wild		9
Gusti	3	01/11/2012	UFM	Semi-Wild		10
Iyos	3	01/11/2012	NSF	Semi-Wild		7
Jamal	3	01/11/2012	UFM	Semi-Wild		10
Kopi	3	01/11/2012	NSF	Semi-Wild		10
Kishi (Offspring of Kopi)	3	01/11/2012		Born in Batikap		0
Mangkutub	3	01/11/2012	UFM	Semi-Wild		10
Paluy	3	01/11/2012	NSF	Semi-Wild		10
Chanel	3	02/11/2012	SAF	Rehabilitant	3	13
Charlie (Offspring of Chanel)	3	02/11/2012	UFM	Born on Island		4
Emen	3	02/11/2012	SAF	Rehabilitant	4	17
Embong (Offspring of Emen)	3	02/11/2012	UFM	Born on Island		3
Gadis	3	02/11/2012	SAF	Rehabilitant	2.5	15
Garu (Offspring of Gadis)	3	02/11/2012	NSF	Born on Island		3
Jamiat	3	02/11/2012	UFM	Rehabilitant	5.5	17
Leonora	3	02/11/2012	SAF	Rehabilitant	3	16
Lamar (Offspring of Leonora)	3	02/11/2012	UFM	Born on Island		3
Menteng	3	02/11/2012	UFM	Rehabilitant	3.5	15
Sif	3	02/11/2012	SAF	Rehabilitant	5	18
Sifa (Offspring of Sif)	3	02/11/2012	NSF	Born on Island		2
Terusan	3	02/11/2012	UFM	Born on Island		8
Centil	4	14/02/2013	SAF	Rehabilitant	6	18
Ross (Offspring of Centil)	4	14/02/2013	NSF	Born on Island		5

Darsi	4	14/02/2013	NSF	Semi-Wild		11
Edwan	4	14/02/2013	UFM	Semi-Wild		9
Klowor	4	14/02/2013	UFM	Semi-Wild		11
Lupita	4	14/02/2013	NSF	Rehabilitant	3.5	13
Markisa	4	14/02/2013	SAF	Rehabilitant	4	17
Manggo (Offspring of Markisa)	4	14/02/2013	NSF	Born on Island		7
Uli (Offspring of Markisa)	4	14/02/2013	NSF	Born on Island		1
Rachmad	4	14/02/2013	UFM	Semi-Wild		9
Dagoy	4	15/02/2013	NSF	Rehabilitant	12	24
Debby (Offspring of Dagoy)	4	15/02/2013	NSF	Born on Island		3
Isis	4	15/02/2013	NSF	Rehabilitant	6.5	16
Lesta	4	15/02/2013	SAF	Rehabilitant	4	18
Lewis (Offspring of Lesta)	4	15/02/2013	NSF	Born on Island		1
Mogok	4	15/02/2013	UFM	Rehabilitant	2	13
Alibaba	4	16/02/2013	UFM	Rehabilitant	1.5	12
Danur	4	16/02/2013	FM	Rehabilitant	4	17
James	4	16/02/2013	FM	Rehabilitant	5	14
Mexa	4	16/02/2013	NSF	Wild		22
Arun	5	16/08/2013	UFM	Rehabilitant	2.5	14
Bule	5	16/08/2013	UFM	Rehabilitant	6	18
Lulu	5	16/08/2013	NSF	Rehabilitant	4	16
Mama Mozzy	5	16/08/2013	SAF	Rehabilitant	12	23
Myzo (Offspring of Mama Mozzy)	5	16/08/2013	NSF	Born on Island		2
Astria	5	17/08/2013	NSF	Born on Island		6
Matilda	5	17/08/2013	SAF	Rehabilitant	3.5	17
Georgina (Offspring of Matilda)	5	17/08/2013	NSF	Born on Island		1
Lona	5	17/08/2013	NSF	Rehabilitant	6	19
Nielsen	5	17/08/2013	NSF	Born on Island		8
Max	5	17/08/2013	FM	Rehabilitant	3	16
Mita	5	17/08/2013	NSF	Rehabilitant	3.5	12
Mongki	5	17/08/2013	UFM	Rehabilitant	4	15
Uban	5	17/08/2013	FM	Rehabilitant	3	16
Bonet	5	18/08/2013	UFM	Rehabilitant	2.5	13
Monmon	5	18/08/2013	NSF	Rehabilitant	4.5	13
Tehang	5	18/08/2013	NSF	Rehabilitant	4	14
Ubai	5	18/08/2013	NSF	Rehabilitant	4	15
Cilik	6	29/11/2013	UFM	Born on Island		6
Cindy	6	29/11/2013	SAF	Rehabilitant	5	19
Riwut (Offspring of Cindy)	6	29/11/2013	NSF	Born on Island		1
Daisy	6	29/11/2013	NSF	Rehabilitant	2	14
Mandra	6	29/11/2013	NSF	Rehabilitant	1	15
Nopi	6	29/11/2013	SAF	Rehabilitant	7	20
Nicky (Offspring of Nopi)	6	29/11/2013	UFM	Born on Island		3
Zona	6	29/11/2013	NSF	Born on Island		9
Bertha	6	30/11/2013	NSF	Rehabilitant	4.5	16
Boy	6	30/11/2013	UFM	Rehabilitant	5	17
Indah	6	30/11/2013	NSF	Born on Island		6
Inung	6	30/11/2013	SAF	Rehabilitant	2.5	15
Ina (Offspring of Inung)	6	30/11/2013	NSF	Born on Island		1
Komo	6	30/11/2013	UFM	Rehabilitant	2	14
Lolin	6	30/11/2013	NSF	Rehabilitant	7	20
Shelli	6	30/11/2013	SAF	Rehabilitant	7	20
Forest (Offspring of Shelli)	6	30/11/2013	NSF	Born on Island		3
Dita	7	07/02/2014	NSF	Rehabilitant	4	17
Halt (Offspring of Dita)	7	07/02/2014	NSF	Born on Island		2
Hamlet	7	07/02/2014	FM	Rehabilitant	3	18

Joys	7	07/02/2014	NSF	Rehabilitant	7.5	19
Judy	7	07/02/2014	NSF	Rehabilitant	6	18
Son (Offspring of Judy)	7	07/02/2014	UFM	Born on Island		2
Kitty	7	07/02/2014	SAF	Rehabilitant	3.5	18
Kate (Offspring of Kitty)	7	07/02/2014	NSF	Born on Island		3
Noor	7	07/02/2014	NSF	Rehabilitant	1	17
Sarita	7	07/02/2014	NSF	Rehabilitant	6	20
Zena	7	07/02/2014	NSF	Rehabilitant	5	18
William (Offspring of Zena)	7	07/02/2014	UFM	Born on Island		4
Jane	7	08/02/2014	NSF	Rehabilitant	3.5	19
Jiro (Offspring of Jane)	7	08/02/2014	UFM	Born on Island		1
Jojang	7	08/02/2014	UFM	Born on Island		7
Jupiter	7	08/02/2014	NSF	Rehabilitant	1	15
Julfa (Offspring of Jupiter)	7	08/02/2014	NSF	Born on Island		1
Manisha	7	08/02/2014	NSF	Rehabilitant	4	19
Mercury	7	08/02/2014	UFM	Rehabilitant	1.5	13
Reno	7	08/02/2014	UFM	Rehabilitant	2	14
Slamet	8	19/04/2014	FM	Rehabilitant	2.5	18
Kacio	8	19/04/2014	NSF	Rehabilitant	2.5	14
Olympia	8	19/04/2014	NSF	Rehabilitant	2	14
Mego	8	19/04/2014	FM	Rehabilitant	3	16
Sella	8	20/04/2014	NSF	Rehabilitant	2.5	14
Trold	8	20/04/2014	NSF	Rehabilitant	1.5	13
Bonita	8	20/04/2014	NSF	Rehabilitant	2	13
Miss Owen	8	20/04/2014	NSF	Rehabilitant	1.5	17
Cuplis	8	20/04/2014	NSF	Semi-Wild		12
Wardah	8	20/04/2014	NSF	Semi-Wild		11
Kiki	8	20/04/2014	NSF	Rehabilitant	6.5	19
Hardi	8	20/04/2014	NSF	Born on Island		7
Maha	9	05/02/2015	UFM	Rehabilitant	2.5	10
Compost	9	27/02/2015	NSF	Rehabilitant	1.5	13
Dewi	9	27/02/2015	NSF	Rehabilitant	6	20
Delta (Offspring of Dewi)	9	27/02/2015	UFM	Born in Batikap		0
Mentos	9	27/02/2015	NSF	Rehabilitant	2	17
Jatihan	9	27/02/2015	UFM	Rehabilitant	2	9
Jambi	10	26/08/2015	SAF	Rehabilitant	2.5	9
Jamartin (Offspring of Jambi)	10	26/08/2015	UFM	Born on Island		2
Sumeh	10	26/08/2015	SAF	Rehabilitant	3.5	19
Sawung (Offspring of Sumeh)	10	26/08/2015	UFM	Born on Island		1
Gembira	10	26/08/2015	NSF	Born on Island		8
Sigi	10	26/08/2015	UFM	Rehabilitant	2.5	11
Mawar	10	26/08/2015	SAF	Rehabilitant	6.5	22
Mumpuni (Offspring of Mawar)	10	26/08/2015	UFM	Born on Island		3
Wombat	10	26/08/2015	UFM	Rehabilitant	2.5	10
Afri	10	26/08/2015	NSF	Rehabilitant	4	19
Mardianto	10	26/08/2015	UFM	Rehabilitant	2.5	13
Benjol	10	27/08/2015	NSF	Rehabilitant	1.5	12
Cetah	10	27/08/2015	NSF	Rehabilitant	2.5	17
Didik	10	27/08/2015	FM	Rehabilitant	3.5	18
Chiki	10	27/08/2015	NSF	Rehabilitant	4	17
Samba	10	27/08/2015	FM	Rehabilitant	1	17
Nora	10	27/08/2015	NSF	Rehabilitant	2	15
Meklies	10	27/08/2015	SAF	Rehabilitant	2.5	12
Meklias (Offspring of Meklies)	10	27/08/2015	UFM	Born on Island		3
Gina	11	13/04/2016	NSF	Rehabilitant	1	16
Zakia	11	14/04/2016	NSF	Rehabilitant	1	13

Kevin	11	15/04/2016	UFM	Rehabilitant	2	15
Sule	11	14/04/2016	NSF	Rehabilitant	2.5	9
Belli	11	18/04/2016	NSF	Rehabilitant	3.5	14
Olivia	11	18/04/2016	NSF	Rehabilitant	1.5	15
Lomon	11	18/04/2016	UFM	Rehabilitant	3.5	14
Ella	11	18/04/2016	NSF	Rehabilitant	2	13
Olbert	11	23/04/2016	UFM	Semi-wild		12
Nobri	11	23/04/2016	NSF	Born on Island		11
Suta	11	23/04/2016	NSF	Semi-wild		12
Sofi	11	23/04/2016	NSF	Semi-wild		15
Bento	12	14/12/2017	FM			
Dani	12	12/12/2017	FM			
Fitun	12	14/12/2017	FM			
Jaki	12	14/12/2017	FM			
Karen	12	14/12/2017	NSF			
Kasper	12	12/12/2017	FM			
Mas	12	12/12/2017	FM			
Sabun	12	12/12/2017	FM			

Appendix B: Profiles of individuals reintroduced into Bukit Baka Bukit Raya National Park

Orangutan Name	Release Group	Release Date	Age-sex	Origin	Age at Rescue	Age at Release
Awa	1	06/08/16	SAF	Rehabilitant	1.5	18
Ewa (Offspring of Awa)	1	06/08/16	NSF	Born on island	0	6
Doren	1	06/08/16	SAF	Rehabilitant	1.3	14
Daichi (Offspring of Doren)	1	06/08/16	UFM	Born on island	0	1
Rambo	1	06/08/16	UFM	Rehabilitant	2	12
Mima	1	08/08/16	NSF	Rehabilitant	2	15
Dara	1	08/08/16	NSF	Rehabilitant	3	14
Kameloh	1	08/08/16	UFM	Rehabilitant	2	11
Winda	1	08/08/16	SAF	Rehabilitant	5	14
Wihim (Offspring of Winda)	1	08/08/16	UFM	Born in NM	0	2
Usro	2	06/10/16	NSF	Semi-Wild	2.5	13
Anggi	2	06/10/16	NSF	Semi-Wild	3	14
Pluto	2	06/10/16	UFM	Rehabilitant	2.5	17
Gurita	2	06/10/16	NSF	Rehabilitant	4	14
Sincan	2	08/10/16	NSF	Semi-Wild	3.5	16
Kumba	2	08/10/16	UFM	Semi-Wild	4.5	14
Ibut	2	08/10/16	UFM	Rehabilitant	2.5	13
Ijum	2	08/10/16	NSF	Semi-Wild	2.5	12
Mini	3	07/12/16	NSF	Rehabilitant	2	16
Juki	3	07/12/16	UFM	Rehabilitant	2	15
Susi	3	07/12/16	NSF	Rehabilitant	2	15
Beda	3	07/12/16	NSF	Rehabilitant	0.1	13
Bana	3	07/12/16	FM	Wild	25	25
Kisar	3	09/12/16	FM	Rehabilitant	2	16
Miri	3	09/12/16	NSF	Rehabilitant	2.5	17
Rina	3	09/12/16	NSF	Rehabilitant	2	15
Sarimin	3	09/12/16	UFM	Rehabilitant	2	13
Sawa	3	09/12/16	SAF	Wild	22	20
Sawi (Offspring of Sawa)	3	09/12/16	NSF	Wild	4	4
Pak Herry	4	15/02/17	FM	Semi-Wild	2	15
Nyiwuh	4	15/02/17	NSF	Rehabilitant	1.5	15

Ine	4	15/02/17	NSF	Semi-Wild	2	14
Besty	4	15/02/17	NSF	Rehabilitant	1	12
Meggi	4	15/02/17	UFM	Rehabilitant	2	13
Sophia	4	15/02/17	NSF	Rehabilitant	2	13
Aulin	4	18/02/17	NSF	Rehabilitant	2.5	14
Eka	4	18/02/17	NSF	Rehabilitant	2	12
Janu	4	18/02/17	UFM	Rehabilitant	1.5	8
Bagio	4	18/02/17	UFM	Semi-Wild	5.5	9
Buntut	4	18/02/17	NSF	Semi-Wild	2	15
Wanna	4	18/02/17	NSF	Rehabilitant	6.5	17
Kato	5	23/05/17	FM	Semi-Wild	2	16
Kipoy	5	23/05/17	NSF	Rehabilitant	3	14
Ranesi	5	23/05/17	NSF	Rehabilitant	4	16
Zoe	5	23/05/17	NSF	Rehabilitant	2.5	16
Carmen	5	23/05/17	NSF	Rehabilitant	1.5	15
Susan	5	23/05/17	NSF	Rehabilitant	2.5	14
Elin	6	03/08/17	NSF	Rehabilitant	2.5	14
Tuhe	6	03/08/17	UFM	Rehabilitant	1.5	15
Cameron	6	03/08/17	NSF	Rehabilitant	1.5	15
Tubagus	6	03/08/17	UFM	Rehabilitant	2.5	15
Geragu	6	03/08/17	NSF	Rehabilitant	2	15
Heidi	6	03/08/17	NSF	Rehabilitant	2.5	14
Niken	6	05/08/17	NSF	Rehabilitant	1.5	19
Pak Edi	6	05/08/17	FM	Rehabilitant	2.5	17
Otong	6	05/08/17	UFM	Rehabilitant	2	16
Suryani	6	05/08/17	NSF	Rehabilitant	2	12
Seruni	6	05/08/17	NSF	Rehabilitant	2	12
Mariam	6	05/08/17	NSF	Rehabilitant	3	11
Hangei	7	10/11/17	NSF	Rehabilitant	4	13
Imot	7	10/11/17	UFM	Rehabilitant	2.5	11
Kahim	7	10/11/17	UFM	Rehabilitant	2	12
Nanga	7	10/11/17	SAF	Rehabilitant	5.5	17
Puji	7	10/11/17	NSF	Rehabilitant	1	11
Puput	7	10/11/17	NSF	Rehabilitant	3	14
Bruni	7	12/11/17	NSF	Rehabilitant	2	11
Rawa	7	12/11/17	UFM	Rehabilitant	3	15
Rebecca	7	12/11/17	NSF	Rehabilitant	2	13
Rowo	7	12/11/17	NSF	Rehabilitant	1.5	15
Stuart	7	12/11/17	UFM	Rehabilitant	1	15
Sukamara	7	12/11/17	NSF	Rehabilitant	9	20
Rutan	8	12/01/18	NSF	Rehabilitant	3	15
Pong	8	12/01/18	UFM	Rehabilitant	2	15
Jaka	8	12/01/18	UFM	Rehabilitant	2	13
Agis	8	12/01/18	NSF	Rehabilitant	2.5	14

Appendix C: Behavioural Ethogram

Order of Activities: 1 = Feeding, 2 = Nest building, 3 = Special behaviours, 4 = Mating behaviours, 5 = Aggressive-dominance, 6 = Social play, 7 = Social groom, 8 = Other social

1. FEEDING	
FEEDING	**F**
CO-FEEDING	**CF**
SUPPLEMENTARY FEEDING	**SF**
FOOD SEARCH	**FS**
Fruit:	
Fruit ripe	FR
Fruit unripe	FUM
Seeds	/ S
Skin	/ SK
Whole fruit	/ WH
Essence	/ ES
unknown part	/ U
Other Foods:	
Flowers	FL
Flower bud	FLB
Mature leaves / other green vegetative matter	L
Leaf shoots	LS
Epiphytes (orchids, ferns etc.)	E
Pith of Rattan Stem	PR
Pith of Pandan	PPN
Pith of Palm (Diwung, Lisum, etc.)	PPL
Pith of Branch / Liana	PBR
Other Pith (suli / grasses etc.)	PI
Bark (cambium)	BK
Roots	RT
Invertebrates (termites, ants, caterpillars etc.)	IV
Honey	HY
Fungi	FG
Meat (vertebrates)	M
Soil	SL
Rotten wood (no termites)	RW
Sap	SAP
Water	W
Mothers Milk	SUSU
Unknown Food	UF

2. NEST BUILDING	
NEST BUILDING	**N**
Day nest	DN
Night nest	NN
New Nest	/ NEN
Rebuilt nest	/ RB
Reused nest	/ RU

3. SPECIAL BEHAVIOURS	
MEDICATION	**ME**
Fur-rubbing	/ FUR
MANIPULATE OBJECT (notes: type, purpose)	**MO**
GIVING BIRTH	**GB**

4. MATING BEHAVIOURS	
SOCIAL	**S**
Sex Investigate	SV
Copulation attempt (primarily males)	CAT
Female resist mating	FRS
Mating / Copulation	MA

5. AGGRESSIVE-DOMINANCE (OU)	
SOCIAL	**S**
Aggressive chase / charge	ACH
Aggressive contact / fighting	ACT
Aggressive branch breaking / shaking / display	ABB
Aggressive snag crashing	ASC
Aggressive kiss squeak	AKS
Long-call	LC
Submissive	SB
Flee	FE

6. SOCIAL PLAY	
PLAY	**P**
Play with other individual	PL
With mother	/ M
With offspring	/ O
With adult	/ A
With infant	/ IN
With adolescent	/ AJ
With other species e.g. Gibbon	/TA

7. SOCIAL GROOM	
GROOM	**G**
Groom other individual	GA
Groomed by other individual	GR
With mother	/ M
With offspring	/ O
With other adult	/ A
With other infant	/ IN
With adolescent	/ AJ

8. OTHER SOCIAL	
SOCIAL	**S**
Touch (non-aggressive contact e.g. hug)	TC
Observe / watch other OU / (close attention to the activities of another)	WC
Beg for food from other OU	BEG
Vocalisation (to / in response to other OU)	V

Order of Activities: 9 = Aggression to other animal, 10 = Aggression to observer, 11 = Infant behaviours, 12 =Travelling, 13 = Self-groom / defecate / urinate, 14 = Resting

9. AGGRESSION TO ANOTHER ANIMAL	
AGGRESSION TOWARDS OTHER ANIMAL	**ATA**
Kiss squeak towards other animal	KS
Threatening other animal, e.g. charge, snagcrash, shaking branches etc.	TH

10. AGGRESSION TO OBSERVER	
AGGRESSION TO OBSERVER	**ATO**
AGGRESSION TO OTHER PERSON	**AOP**
Kiss squeak towards observer / other person	KSTO
Threatening observer / other person (shake branch, throw, charge)	THTO
Chase / charge observer	CHO
INTERACTION WITH OBSERVER	**IWO**
Atempt to touch	AT
Touch	TC
Beg for food	BEG
Watch Observer	OOP

11. 'INFANT' BEHAVIOURS	
PLAY	**P**
Independent play, e.g. swinging, twirling	IPS
Independent play with object	IPO
INFANT ACTIVITIES	**AKA**
Observe / watch mother (close attention to the activities of the mother)	OM
Try Food (try / taste without really eating)	FT
Beg for food (from mother)	BEG
Soft hoot / whimper	HW
Cry	CY

12. TRAVELLING	
TRAVELLING	**T**
Tree sway	TT
Clambering	CLA
Climbing / Descending	CLI
Brachiating	BR
Quadrupedal Walking	QW
Bipedal Walking	BI

13. SELF-GROOM / DEFECATE / URINATE	
GROOM	**G**
Self-groom	SG
DEFECATE / URINATE	**DU**

14. RESTING	
RESTING	**R**
Sitting	SI
Standing	ST
Lying Down	LD
Hanging	HA
Quadrupedal	Q
Tree / branch	/ TR
Liana	/ LI
Ground	/ G
Nest	/ N
On mother (infant)	/ M
Clinging ventrally	CLV
Clinging dorsally	CLD

LOST	**L**
UNKNOWN	**U**
OTHER (describe)	**O**

Note: Unknown (U) and Other (O) can be used as primary activity or secondary activity

Height
0m (on ground); 1-5m; 6-10m; 11-15m; 16-20m 21-25m, 26-30m, 31-35m, 36-40m, 41-45m….

Proximity	
Proximity 0 (contact)	0
Proximity less than 2m (no contact)	<2
Proximity 2-5m	<5
Proximity 6-10m	<10
Proximity 11-20m	<20
Proximity 21-50m	<50
Proximity greater than 50m (out of sight)	>50

Appendix D: Example of behavioural data collection sheet.

Date:			**Name of Focal OU**				**Observer:**					**GPS Name:**		
Time	***Primary Activity FOCAL***	***Secondary Activity FOCAL***	***Species Eaten by FOCAL***	***Height of FOCAL***	***Primary Activity OFFSPRING***	***Secondary Activity OFFSPRING***	***Species Eaten by OFFSPRING***	***Height of OFFSPRING***	***Prox. Mother-Offspring***	***Same tree as mother ?***	***GPS***	***# KS***	***Party size***	***Comments (Party members)***
4.45														
4.50														
4.55														
5.00														
5.05														
5.10														
5.15														
5.20														
5.25														
5.30														
…														

Appendix E: Tables of statistical results from linear mixed model analyses of feeding levels

TNBBBR — ***Feeding***

	Full Model			*Model (-Trimester)*			*Model (-AgeSex)*		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	28.64	16.87 – 40.42	**<0.001**	27.06	12.48 – 41.63	**<0.001**	35.24	31.29 – 39.18	**<0.001**
Trimester 2	17.95	12.55 – 23.35	**<0.001**				18.15	12.78 – 23.53	**<0.001**
Trimester 3	21.98	15.93 – 28.04	**<0.001**				22.08	16.03 – 28.14	**<0.001**
Trimester 4	19.29	12.28 – 26.29	**<0.001**				19.55	12.52 – 26.58	**<0.001**
Trimester 5	18.95	10.19 – 27.71	**<0.001**				20.07	11.26 – 28.88	**<0.001**
Trimester 6	27.07	14.95 – 39.20	**<0.001**				27.68	15.57 – 39.79	**<0.001**
NSF	9.14	-3.04 – 21.32	0.141	20.83	6.28 – 35.37	**0.005**			
SAF	-0.50	-15.22 –14.22	0.947	14.54	-282 – 31.90	0.101			
UFM	4.65	-7.98 – 17.27	0.471	16.03	0.95 – 31.11	**0.037**			
Random Effects									
σ^2	159.57			254.34			158.76		
τ_{00}	14.44 $_{Name}$			3.95 $_{Name}$			22.33 $_{Name}$		
	5.72 $_{RG}$			19.23 $_{RG}$			11.36 $_{RG}$		
ICC	0.08 $_{Name}$			0.01 $_{Name}$			0.12 $_{Name}$		
	0.03 $_{RG}$			0.07 $_{RG}$			0.06 $_{RG}$		
Observations	161			161			**161**		
Marginal R^2/ Conditional R^2	0.387/ 0.456			0.058/ 0.137			**0.353/ 0.466**		

Batikap — ***Feeding***

	Full Model			*Model (-Trimester)*			*Model (-AgeSex)*		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	26.49	17.12 – 35.87	**<0.001**	37.52	27.30 – 47.75	**<0.001**	32.75	27.92 – 37.59	**<0.001**
Trimester 2	19.50	14.15 – 24.86	**<0.001**				19.71	14.34 – 25.09	**<0.001**
Trimester 3	19.30	13.47 – 25.13	**<0.001**				19.24	13.39 – 25.08	**<0.001**
Trimester 4	22.23	16.09 – 28.38	**<0.001**				22.26	16.09 – 28.43	**<0.001**
Trimester 5	17.00	10.10 – 23.91	**<0.001**				16.91	9.97 – 23.84	**<0.001**

Trimester 6	19.35	12.56 – 26.13	**<0.001**				19.60	12.79 – 26.41	**<0.001**
Trimester 7	21.35	13.92 – 28.79	**<0.001**				21.66	14.19 – 29.12	**<0.001**
Trimester 8	16.88	9.31 -24.46	**<0.001**				17.26	9.66 – 24.86	**<0.001**
Trimester 9	13.51	4.09 – 22.93	**0.005**				13.64	4.19 – 23.10	**0.005**
Trimester 10	13.61	4.15 – 23.07	**0.005**				14.22	4.73 – 23.71	**0.003**
Trimester 11	8.15	-2.53 – 18.84	0.135				8.19	-2.54 – 18.92	**0.135**
Trimester 12	17.77	-2.53 – 18.84	**0.002**				18.30	6.95 – 29.65	**0.002**
Trimester 13	13.77	6.46 – 29.07	**0.024**				13.80	1.77 – 25.83	**0.025**
Trimester 14	19.82	1.79 – 25.75	**0.001**				19.99	8.57 – 31.42	**0.001**
Trimester 15	24.06	8.44 – 31.19	**<0.001**				24.62	11.76 – 37.49	**<0.001**
Trimester 16	21.03	11.23 – 36.88	**0.001**				21.47	9.46 – 33.48	**<0.001**
Trimester 17	29.42	9.07 – 33.00	**<0.001**				29.17	15.04 – 43.29	**<0.001**
Trimester 18	35.94	15.35 – 43.48	**<0.001**				25.99	24.52 – 47.46	**<0.001**
Trimester 19	29.66	24.52 – 47.36	**<0.001**				30.16	14.63 – 45.68	**<0.001**
Trimester 20	32.29	14.19 – 45.14	**<0.001**				32.17	17.91 – 46.44	**<0.001**
Trimester 21	13.83	18.08 – 46.49	0.058				13.64	-0.74 – 28.03	0.063
Trimester 22	20.78	7.41 – 34.15	**0.002**				21.05	7.62 – 34.48	**0.002**
Trimester 23	10.51	-11.08 – 32.10	0.340				10.99	-10.69 – 32.67	0.320
NSF	8.79	-0.51 – 18.09	0.064	10.65	-0.09 – 21.39	0.052			
SAF	6.73	-3.00 – 16.46	0.175	10.28	0.99 -21.56	0.074			
UFM	3.56	-6.06 – 13.18	0.468	5.73	-5.41 – 16.86	0.313			
Random Effects									
σ^2	220.51			287.50			222.28		
τ_{00}	56.67 Name			84.82 Name			59.49 Name		
	31.03 RG			22.16 RG			32.67 RG		
ICC	0.18 Name			0.22 Name			0.19 Name		
	0.10 RG			0.06 RG			0.10 RG		
Observations	412			412			**412**		
Marginal R^2/ Conditional R^2	0.224/ 0.445			0.022/ 0.287			**0.209/ 0.441**		

Appendix F: Tables of statistical results from linear mixed model analyses of resting levels

TNBBBR — ***Resting***

	Full Model			*Model (-Trimester)*			*Model (-AgeSex)*		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	46.40	35.98 – 56.83	**<0.001**	46.84	34.67 – 59.00	**<0.001**	39.58	35.72 – 43.44	**<0.001**
Trimester 2	-13.26	-18.08 – -8.45	**<0.001**				-13.51	-18.25 – -8.76	**<0.001**
Trimester 3	-16.97	-22.38 – -11.56	**<0.001**				-17.18	-22.55 – -11.82	**<0.001**
Trimester 4	-12.67	-18.91 – -6.43	**<0.001**				-12.98	-19.20 – -6.76	**<0.001**
Trimester 5	-13.10	-20.90 – -5.31	**<0.001**				-14.15	-21.94 – -6.37	**<0.001**
Trimester 6	-21.99	-32.78 – -11.19	**<0.001**				-22.78	-33.48 – -12.08	**<0.001**
NSF	-9.25	-19.97 – 1.47	0.091	-17.59	-29.86 – -5.31	**0.005**			
SAF	-0.02	-12.93 – 12.90	0.998	-10.48	-24.93 – 3.98	0.155			
UFM	-5.34	-16.46 – 5.78	0.346	-13.03	-25.73 – -0.32	**0.044**			
Random Effects									
σ^2	126.91			183.24			122.54		
τ_{00}	7.63 $_{Name}$			1.59 $_{Name}$			18.46 $_{Name}$		
	6.63 $_{RG}$			7.40 $_{RG}$			14.49 $_{RG}$		
ICC	0.05 $_{Name}$			0.01 $_{Name}$			0.12 $_{Name}$		
	0.05 $_{RG}$			0.04 $_{RG}$			0.09 $_{RG}$		
Observations	161			161			**161**		
Marginal R^2/ Conditional R^2	0.322/ 0.390			0.068/ 0.111			**0.277/ 0.430**		

Batikap — ***Resting***

	Full Model			*Model (-Trimester)*			*Model (-AgeSex)*		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	52.01	44.33 – 59.68	**<0.001**	44.01	35.98 – 52.05	**<0.001**	39.77	35.71 – 43.82	**<0.001**
Trimester 2	-12.30	-16.86 – -7.74	**<0.001**				-12.59	-17.21 – -7.97	**<0.001**
Trimester 3	-14.56	-19.52 – -9.60	**<0.001**				-14.54	-19.57 – -9.52	**<0.001**
Trimester 4	-13.38	-18.61 – -8.15	**<0.001**				-12.99	-18.29 – -7.68	**<0.001**
Trimester 5	-11.73	-17.61 – -5.84	**<0.001**				-11.19	-17.16 – -5.23	**<0.001**

Trimester 6	-12.87	-18.65 – -7.08	**<0.001**				-13.04	-18.90 – -7.18	**<0.001**
Trimester 7	-15.80	-22.13 – -9.47	**<0.001**				-15.92	-22.34 – -9.50	**<0.001**
Trimester 8	-14.54	-20.99 – -8.08	**<0.001**				-14.50	-21.04 – -7.97	**<0.001**
Trimester 9	-7.18	-15.21 – 0.85	0.080				-7.25	-15.39 – 0.88	0.081
Trimester 10	-14.14	-22.20 – -6.08	**0.001**				-14.43	-22.59 – -6.26	**0.001**
Trimester 11	-5.44	-14.55 – 3.68	0.242				-5.05	-14.29 – 4.18	0.284
Trimester 12	-9.46	-19.10 – 0.18	0.054				-9.81	-19.58 – -0.05	**0.049**
Trimester 13	-13.14	-23.35 – -2.92	**0.012**				-12.87	-23.23 – -2.52	**0.015**
Trimester 14	-19.18	-28.86 – -9.49	**<0.001**				-19.56	-29.39 – -9.73	**<0.001**
Trimester 15	-16.14	-27.09 – -5.19	**0.004**				-16.33	-27.40 – -5.25	**0.004**
Trimester 16	-16.46	-26.67 – -6.24	**0.002**				-16.68	-27.02 – -6.35	**0.002**
Trimester 17	-17.90	-29.90 – -5.91	**0.003**				-18.15	-30.30 – -6.00	**0.003**
Trimester 18	-21.06	-30.80 – -11.33	**<0.001**				-21.11	-30.98 – -11.25	**<0.001**
Trimester 19	-22.12	-35.34 – -8.90	**0.001**				-22.28	-35.65 – -8.91	**0.001**
Trimester 20	-17.92	-30.03 – -5.81	**0.004**				-18.19	-30.47 – -5.92	**0.004**
Trimester 21	-20.46	-32.65 – -8.28	**0.001**				-20.82	-33.18 – -8.45	**0.001**
Trimester 22	-14.18	-25.52 – -2.83	**0.014**				-14.98	-26.52 – -3.44	**0.011**
Trimester 23	-7.96	-26.42 – 10.50	0.398				-8.22	-26.89 – 10.44	0.388
NSF	-15.45	-23.07 – -7.84	**<0.001**	-16.73	-24.97 – -8.49	**<0.001**			
SAF	-9.51	-17.46 – -1.57	**0.019**	-11.83	-20.40 – -3.26	**0.007**			
UFM	-13.07	-20.96 – -5.19	**0.001**	-14.41	-22.93 – -5.90	**0.001**			
Random Effects									
σ^2	161.76			196.11			164.99		
τ_{00}	33.15 Name			37.70 Name			41.66 Name		
	18.92 RG			22.49 RG			21.66 RG		
ICC	0.16 Name			0.15 Name			0.18 Name		
	0.09 RG			0.09 RG			0.10 RG		
Observations	412			412			**412**		
Marginal R^2/ Conditional R^2	0.200/ 0.395			0.058/ 0.280			**0.149/ 0.386**		

Appendix G: Tables of statistical results from linear mixed model analyses of travelling levels

TNBBBR — ***Travelling***

	Full Model			*Model (-Trimester)*			*Model (-AgeSex)*		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	22.56	17.56 – 27.56	**<0.001**	22.97	17.40 – 28.54	**<0.001**	21.71	20.08 – 23.34	**<0.001**
Trimester 2	-3.48	-5.79 – -1.17	**0.003**				-3.57	-5.85 – -1.30	**0.002**
Trimester 3	-4.16	-6.76 – -1.56	**0.002**				-4.26	-6.82 – -1.70	**<0.001**
Trimester 4	-8.02	-11.02 – -5.02	**<0.001**				-8.12	-11.09 – -5.16	**<0.001**
Trimester 5	-7.11	-10.85 – -3.36	**<0.001**				-7.17	-10.89 – -3.46	**<0.001**
Trimester 6	-4.96	-10.14 – -3.36	0.061				-5.04	-10.15 – 0.08	0.054
NSF	-0.78	-5.89 – 4.33	0.765	-3.58	-9.03 – 1.87	0.198			
SAF	-1.18	-7.34 – 4.97	0.706	-3.92	-10.45 – 2.60	0.238			
UFM	-1.16	-6.46 – 4.15	0.669	-4.07	-9.73 – 1.59	0.159			
Random Effects									
σ^2	29.20			36.28			28.99		
τ_{00}	1.33 $_{Name}$			0.00 $_{Name}$			1.67 $_{Name}$		
	2.03 $_{RG}$			4.74 $_{RG}$			1.96 $_{RG}$		
ICC	0.04 $_{Name}$			0.00 $_{Name}$			0.05 $_{Name}$		
	0.06 $_{RG}$			0.12 $_{RG}$			0.06 $_{RG}$		
Observations	161			161			**161**		
Marginal R^2/ Conditional R^2	0.203/ 0.285			0.011/ 0.126			**0.203/ 0.291**		

Batikap — ***Travelling***

	Full Model			*Model (-Trimester)*			*Model (-AgeSex)*		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	15.74	11.47 – 20.00	**<0.001**	12.44	7.95 – 16.94	**<0.001**	19.83	18.04 – 21.62	**<0.001**
Trimester 2	-5.67	-8.11 – -3.22	**<0.001**				-5.52	-7.97 – -3.08	**<0.001**
Trimester 3	-4.78	-7.45 – -2.12	**<0.001**				-4.60	-7.27 – -1.93	**0.001**
Trimester 4	-7.92	-10.73 – -5.11	**<0.001**				-7.98	-10.80 – -5.16	**<0.001**
Trimester 5	-5.20	-8.37 – -2.04	**0.001**				-5.27	-8.43 – -2.10	**0.001**

Trimester 6	-6.62	-9.73 – -3.51	**<0.001**				-6.49	-9.60 – -3.38	**<0.001**
Trimester 7	-5.33	-8.75 – -1.92	**0.002**				-5.23	-8.64 – -1.81	**0.003**
Trimester 8	-5.45	-8.91 – -1.98	**0.002**				-5.42	-8.89 – -1.96	**0.002**
Trimester 9	-4.30	-8.61 – 0.01	0.051				-4.08	-8.39 – 0.23	0.064
Trimester 10	-8.90	-13.24 – -4.57	**<0.001**				-8.80	-13.14 – -4.46	**<0.001**
Trimester 11	-3.28	-8.17 – 1.61	0.189				-3.26	-8.15 – 1.63	0.192
Trimester 12	-8.75	-13.93 – -3.58	**0.001**				-8.63	-13.80 – -3.46	**0.001**
Trimester 13	-6.22	-11.71 – -0.74	**0.026**				-6.13	-11.61 – -0.65	**0.028**
Trimester 14	-9.23	-14.44 – -4.01	**0.001**				-8.95	-14.17 – -3.73	**0.001**
Trimester 15	-10.22	-16.08 – -4.36	**0.001**				-10.11	-15.96 – -4.26	**0.001**
Trimester 16	-10.17	-15.64 – -4.70	**<0.001**				-10.04	-15.50 – -4.57	**<0.001**
Trimester 17	-11.47	-17.92 – -5.03	**<0.001**				-11.05	-17.50 – -4.61	**0.001**
Trimester 18	-14.73	-19.95 – -9.51	**<0.001**				-14.45	-19.66 – -9.24	**<0.001**
Trimester 19	-9.84	-16.92 – -2.77	**0.006**				-9.64	-16.70 – -2.59	**0.007**
Trimester 20	-11.79	-18.28 – -5.29	**<0.001**				-11.33	-17.82 – -4.84	**0.001**
Trimester 21	-7.73	-14.29 – -1.17	**0.021**				-7.10	-13.67 – -0.54	**0.034**
Trimester 22	-9.75	-15.87 – -3.62	**0.002**				-9.27	-15.41 – -3.13	**0.003**
Trimester 23	-9.46	-19.32 – 0.40	0.060				-9.21	-19.05 – 0.64	0.067
NSF	3.94	-0.46 – 8.35	0.080	2.86	-2.01 – 7.73	0.250			
SAF	4.02	-0.63 – 8.67	0.090	2.55	-2.61 – 7.70	0.333			
UFM	5.77	1.17 – 10.36	**0.014**	4.69	-0.40 – 9.79	0.071			
Random Effects									
σ^2	45.84			54.26			45.59		
τ_{00}	15.72 Name			22.39 Name			18.68 Name		
	1.93 RG			0.00 RG			1.40 RG		
ICC	0.25 Name			0.29 Name			0.28 Name		
	0.03 RG			0.00 RG			0.02 RG		
Observations	412			412			**412**		
Marginal R^2/ Conditional R^2	0.172/ 0.402			NA			**0.149/ 0.409**		

Appendix H: Tables of statistical results from generalised linear mixed model analyses of party size

TNBBBR

	0-3 months		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	2.20	1.80 – 2.69	**<0.001**
Month Post-Release	0.77	0.72 – 0.82	**<0.001**
Random Effects			
σ^2	0.51		
$T_{00\ Follow\ Number}$	0.18		
$T_{00\ ID}$	0.05		
$T_{00\ Age}$	0.02		
$ICC_{Follow\ Number}$	0.23		
ICC_{ID}	0.07		
ICC_{Age}	0.03		
Observations	35431		
Marginal R^2/ Conditional R^2	0.039/ 0.352		

TNBBBR

	4-12 months		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	1.17	1.06 – 1.29	**0.002**
Month Post-Release	1.00	0.99 – 1.01	0.442
Random Effects			
σ^2	0.63		
$T_{00\ Follow\ Number}$	0.09		
$T_{00\ ID}$	0.00		
$T_{00\ Age}$	0.00		
$ICC_{Follow\ Number}$	0.13		
ICC_{ID}	0.00		
ICC_{Age}	0.00		
Observations	24836		
Marginal R^2/ Conditional R^2	0.000/ 0.128		

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